Growth of understory spruce following mountain pine beetle attack and recalibration and validation of the Mixedwood Growth Model for black spruce

by

Felix Osagie Oboite

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University of Alberta

Abstract

Effective forest management requires reliable growth and yield models and adequate information on changes in the forest resulting from climate change, insect outbreak and competition from neighboring trees. Growth responses of white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) B.S.P) were examined in mountain pine beetle affected stands in the lower foothills of western Alberta, Canada. Diameter and height growth increased after release with white spruce responding a year earlier as well as having a higher mean growth than black spruce. Post-release diameter and height growth were also affected by initial sizes of trees (positive effect), and age (negative effects). High spruce/fir densities resulted in increased height growth and reduction in diameter growth of both spruces. Spruce/fir tree density assessed with a plot radius of 5.64m and their spatial distribution was more adequate for estimating understory light than 3.99m plot radius. While both spruces have the potential to replace dead pine trees, thinning may be needed in areas where high spruce/fir densities might result in competitive suppression of growth. In the second component of this study, long term measurement data collected across western Canada and Alaska were used for this study to characterize the effects of deciduous and coniferous competition and climate on growth and mortality of black spruce. A non-linear mixed model and a generalized logistic function were used to develop growth and mortality functions, respectively. Results showed that climate was a very important predictor in growth and mortality models. Temperature related variables (mean annual temperature and frost free period) increased diameter and height growth while moisture related variables (climate moisture index and mean annual precipitation) had negative effects. Coniferous competition (pine and spruce/fir) negatively affected growth while deciduous competition showed a positive influence suggesting that deciduous trees may be compatible with black spruce because they utilize different niches and/or due to facilitative effects of deciduous. The positive effect of deciduous on black spruce growth might be due to smaller mean densities (tree per hectare) of deciduous competition (369) compared to pine (1263) and spruce (4355) competition that affected growth negatively. Pine competition had stronger effects on black spruce mortality than did deciduous and spruce/fir competition. Black spruce trees allocated more growth to diameter than height or volume when they are larger in size and in wetter sites (higher moisture index and precipitation) with less spruce/fir competition. Finally, models developed in this study were incorporated into the Mixedwood Growth Model (MGM) and results of validation for Alberta and Saskatchewan suggest that the recalibrated version of MGM works better than the earlier version with only a slight bias for stand volume and basal area. This clearly shows that predictions from this new version of MGM can reliably simulate black spruce growth across a range of stand conditions in western Canada.

Preface

This thesis is my original work. My supervisor (Dr Phil Comeau) contributed by providing comments and suggestions for revisions of the drafts of all chapters of this thesis. I collected measurement data for Chapter 2 while PSP data were made available for Chapter 3, 4 and 5. I was responsible for the statistical analysis, methodology, write-up and organization of all of Chapters of this thesis.

To my lovely parents,

Emmanuel Aghafekokhian Oboite

and

Mercy Ofure Oboite

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Table of Contents

List of Tables

List of Figures

Table of Abbreviations

AHM	annual heat moisture
AIC	akaike information criterion
AMB	average mean bias
ASRD	Alberta sustainable resource development
AUC	area under curve
BAL	basal area larger per hectare
CAR1	continuous autoregressive structure
CI	competition index
CMD	climate moisture deficit
CMI	climate moisture index
CRi	crowding index
DBH	diameter at breast height
DImax	maximum diameter increment
EF	efficiency
FFP	frost free period
GP	Grand prairie
H/D	height-diameter ratio
HImax	maximum height increment
KS	Kolmogorov Smirnov
L	length of growth interval
MAE	mean absolute error
MAP	mean annual precipitation
MAT	mean annual temperature
MCDH	modified compatible diameter-height growth model
MCDV	modified compatible diameter-volume growth model
ME	mean error
MGM	mixedwood growth model
MPB	mountain pine beetle
MSP	mean summer precipitation

PAI	periodic annual increment
PGYI	provincial growth and yield initiative
PSP	permanent sample plot
RE	relative error
RI	release intensity
RMB	relative model bias
RMSE	root mean square error
Sb	black spruce
SHM	summer heat moisture
Sw	white spruce
WC	Whitecourt

Chapter 1: Introduction

Black spruce (*Picea mariana* (Mill.) B.S.P) and white spruce (*Picea glauca* (Moench) Voss) are common and widely distributed tree species in the boreal forests of North America (Attree et al. 1991). Black spruce is a shade-tolerant species, while white spruce is normally considered to be moderately shade-tolerant (Grossnickle 2000), and both species attain their maximum growth on mesic to subhygric sites (Burns and Honkala 1990). However, the two species are generally found on different soil types with black spruce being more common on peaty organic soils and white spruce being more common on mineral soils (brunisolic and luvisolic). Black and white spruces are important wood fiber sources for the pulp and paper and the lumber industries in Canada (Butos et al. 2008). Their growth rate is dependent on biotic factors such as genetics, photosynthetic capability, and physiological performance (Prasad 1997; Larcher 2003; Otis Prud'homme et al. 2017), as well as potentially limiting abiotic factors such as light, temperature, soil water, and nutrients (Bonan and Shugart 1989; Prasad 1997; Larcher 2003; Kabzems et al. 2016). Because of their importance in the boreal forest a better understanding of how disturbances and climate influence their growth and survival is needed. Disturbances include competition, pathogen and insect attacks, mechanical failure, climate-induced environmental stress, and localized edaphic constraints (Franklin et al. 1987; Waring 1987). Forecasting responses of forest stands to these disturbances, requires forest growth and yield models that incorporate effects of important factors on tree growth and mortality (Husch et al. 1982; Philip 1998).

Broadly, there are two major issues that need to be addressed. Firstly, there are uncertainties regarding how to improve forest management strategies in mitigating the effect of mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) in lodgepole pine (*Pinus contorta* var. latifolia Engelm.) forests in Alberta.

The MPB has the lodgepole pine (*Pinus contorta*) as its primary host, it feeds on and reproduces inside of its pine tree hosts (Wulder et al., 2006a). When they bore into a host tree, an aggregation pheromone is emitted which attracts other beetles in the area (Six et al., 2014). Although attacked trees generally have some defenses, trees can become vulnerable due to low vigour or when there is a high population density of MPB, in such situations, beetles can overcome a tree's defenses (Raffa et al. 2008).

Advance regeneration of spruce might be a valuable method of replacing these affected stands if their growth is properly understood. According to Morin (1994) and Dhar and Hawkins (2011), advanced regeneration is the major source of canopy replacement and change of forest structure under natural or unmanaged conditions following MPB outbreaks. These forests have a structure and composition different from managed forest or forest emanating from other kinds of disturbances (Burton 2006; Griesbauer and Green 2006). Therefore, these differences or future forest conditions need to be considered before taking any further management initiatives (Dhar and Hawkins 2011). For white spruce and black spruce in lodgepole pine dominated stands, it is unclear how they will respond after MPB outbreaks in Alberta. Although there have been some studies on advance regeneration in British Columbia (Dhar and Hawkins 2011; Hawkins et al. 2013; Campbell and Antos 2015; Dhar et al. 2016), there are no detailed published studies on responses of white spruce and black spruce advance regeneration in Alberta. In addition, conditions (soil, ecosite, climate, stand structure etc) that influence tree growth in BC would differ from Alberta (Carroll et al. 2006). Therefore, it is important to quantify the growth of the spruce advance regeneration following MPB outbreaks in Alberta since there is need to maintain forest structure and diversity and maintain a source of mid-term timber supply in affected stands.

Secondly, the Mixedwood Growth Model (MGM) is a stand growth model developed to help forest managers make growth and yield projections for various management options (Bokalo et al. 2012; Bokalo et al. 2013). MGM can project and evaluate growth and yield of important economic tree species for boreal forest which includes white spruce, black spruce, trembling aspen, lodgepole pine, jack pine and mixedwood stands in Alberta, British Columbia, Saskatchewan, and Manitoba (Bokalo 2012; Bokalo et al. 2013). Since calibration of MGM for black spruce was completed in 2003 using a much smaller dataset than is now available, there is need to recalibrate and refine the MGM for black spruce. The recalibration process entails developing models that would be utilized in MGM for stand projection. As part of projecting changes in the black spruce forest, it is unclear how growth and mortality of black spruce are affected by climate, and competition in western Canada. Quantifying the influence of the aforementioned factors will be useful in parameterizing MGM. Tree mortality in the boreal forest is strongly influenced by competition (Yang et al. 2003; Cortini et al. 2017), and drought (Hogg and Wein 2005; Peng et al. 2011; Cortini et al. 2017). With potential future climate warming, tree mortality rates in western Canada are predicted to be more severe than those in eastern Canada due to higher drought stress (Peng et al. 2011). Although, climate variables are not currently included in MGM, they have a strong effect on growth (Cortini et al. 2017) and this is because under the current increases in average temperatures, species better suited to warmer climates might become stronger competitors for resources (Spittlehouse 2008).

In Chapter number two, I examined the diameter and height growth responses of black and white spruce following death of overstory lodgepole pine following MPB outbreaks. The MPB is a native insect that attacks pines in western North American forests; the epidemic peaked in 2005 in British Columbia resulting in huge losses in merchantable volume (Natural Resources Canada 2016). In 2006, beetles from the massive epidemic in central British Columbia were transferred on upper atmospheric winds across the barrier posed by the Rocky Mountains. The beetle is currently established in lodgepole (*Pinus contorta* var. latifolia Engelm.) and jack (*Pinus banksiana* Lamb) pine forests in northern Alberta and threatens to expand east across Canada's boreal forest if conditions are suitable (Natural Resources Canada 2016). The MPB has also moved northwards and in 2012 was reported north of 60° latitude in the Northwest Territories for the first time, although the fate of this small population is uncertain (Natural Resources Canada 2016). The frequency and severity of insect epidemic plays a major role in the structural, biological, and genetic diversity of the forest (Bergeron et al. 1998) and the severity of the insect outbreak has implication for forest regeneration (Diskin et al. 2011; Dhar and Hawkins 2011).

Overstory mortality caused by these beetles creates canopy gaps and can favour the release of understory trees which have been suppressed in the stand (Heath and Alfaro 1990; Axelson et al. 2009). In some areas, spruce exist in the understory of pine dominated stands, and they benefit from the presence of a continuous or partial forest cover that provide a suitable microclimate (Grayson et al. 2012). This sheltered ecological niche is beneficial, and sometimes extremely important to the regeneration of many conifer species that naturally establish in the understory. These advance regeneration can readapt their crown to changes in light following disturbance (McCarthy 2001; Dumais and Prévost 2014). Some advantages of preserving advance regeneration include: 1) it is a low cost alternative for securing adequate regeneration that is well suited to the site; and, 2) it is source of immediate growing stock, shade for subsequent seedlings, hiding cover for wildlife, aesthetics, and some soil protection (McCaughey and Ferguson 1988). Therefore, retention of existing advance regeneration in forest stands after disturbance has achieved some importance in North America (Doucet and Weetman 1990; Dhar and Hawkins 2011; Campbell and Antos 2015; Danyagri et al. 2017).

Interestingly, it may be possible to identify biologically based indicators to assess the release potential of advance regeneration at different developmental stages. The severity of the disturbance has implications to the subsequent growth of understory species. According to Zhang et al. (2013), when openings of the canopy are too rapid or large, it can result to stress and delay growth. Ruel et al. (2000) suggested that age–height growth relationships may be controlled by the live crown of a tree, which is a good indicator for release potential (Ruel et al. 1995). Other potential tree release indicators may include species, logging damage, pre-release height growth, height-to-diameter ratios (Sharma et al. 2016), the number of internodal and nodal branches (Murphy et al. 1999; Ruel et al. 2000). Model projections have indicated that well distributed and healthy advance regeneration in post-MPB stands can contribute harvestable volumes of 200–300 m^3/ha within 25–40 years (Coates et al. 2006) and SORTIE-ND model projections by Coates and Hall (2005) revealed that understory spruce in MPB attacked stands can recover to pre-attack basal areas within 50 years in some experimental sites in British Columbia. Similarly, another SORTIE-ND projection by Pousette (2010) indicated that stands resulting from MPB outbreak can provide mid-term merchantable volumes within 30 years. Growth and yield, and stocking criteria (species composition and spatial distribution) of advance regeneration have management implications for post-MPB attacked stands (Griesbauer and Green 2006) and this might compensate the forest manager for the loss due to MPB. Therefore, this study explored various factors that will affect both diameter and height growth of advance growth after MPB attack.

In Chapter number three, I examine the effect of climate and competition on the growth and mortality of black spruce. Since climate influences important physiological and phenological processes in trees (Kramer et al. 2000; Kozlowski 2002; Walther 2003), climate change may alter these processes, leading to alterations in species distribution, forest composition, resilience, and productivity (Kramer et al. 2000; Bertrand and Castonguay 2003). A better understanding of tree growth– climate relationships may help in predicting the potential impacts of climate change on forest ecosystems (Hamrick 2004; Spittlehouse 2005). Information on climate–growth relationships can be a valuable asset to forest managers developing forest management strategies to adapt to climate change (Littell et al. 2011). Rising temperatures increase the availability of soil nitrogen, which combined with a longer growing season is expected to increase overall tree growth/biomass production (Parker et al. 2000; Strömgren and Linder 2002). However, on some sites, temperature-induced drought stress and reduced tree growth may occur as a result of increases in temperature (Wilmking et al. 2004; Wilmking and Juday 2005). Even small changes in climate will greatly affect growth and survival of forest tree populations in the future with magnitude and type of effect (such as beneficial or detrimental) depending on the species (Rehfeldt et al. 1999, 2002). Therefore, it is important to increase our knowledge of climate–growth relationships, in particular, the factors affecting forest growth and their sensitivity to climatic variables (Crookston et al. 2008, 2010; Itter et al. 2017). When climate variables are not included in growth models like MGM, the implicit assumption is that the rate of tree growth observed when the data used to calibrate the model were collected will remain constant in the future (Crookston et al. 2008). Consequently, predictions from these kind of models are insensitive to changes in climate (Subedi and Sharma 2013).

Changes in forest stand dynamics are usually gradual, but in certain situations (pest or pathogen outbreaks) tree mortality may be very sudden (Waring 1987). Mortality is an important process in stand dynamics and forest succession (Franklin et al. 1987; Kimmins 2004) which is often characterized as a complex process that is difficult to quantify (Hawkes 2000). The accurate prediction of mortality is an essential feature of most forest stand growth models (Yang et al. 2003; Zhao et al. 2004). A number of factors influence the mortality of shade tolerant species like black spruce, and understanding these factors and incorporating them into growth models will help improve predictive ability of our models since reliable predictions of mortality rates are essential to the accurate prediction of stand dynamics. Although patterns and causes of tree death are complex, and mortality predictions are complicated (Franklin et al. 1987), some generalities can be derived and tree mortality can often be modelled successfully using parameters such as relative tree size, stand density, competition and individual tree growth rates (Hamilton 1986). A number of complex mortality models have been developed over the years, for various tree species and stand types. For example, an individual tree mortality model is commonly based on logistic regression and it gives predicted annual survival probability using tree and stand level attributes (and their combinations) such as tree stem diameter and diameter increment, stand basal area, site productivity index, and species composition (Yang et al. 2003; Reyes-Hernandez and Comeau 2014; Cortini et al. 2017).

In the application of growth and yield models, diameter at breast height (DBH) and total height are important (Sharma and Parton 2007) and, it is often possible to predict one from the other because the relationship between diameter and height is often affected by competition from surrounding trees which is constantly changing in response to the dynamics of the ecosystem (Seidel 1984; Nunifu 2009). However, according to Nunifu (2009), an aspect of compatibility often ignored in most of these growth and yield studies is the compatibility in height–diameter relationships of the individual trees in relation to stand structure and density. The incompatible prediction of individual tree diameter and height growth may result in tree height–diameter ratios that are not consistent with the stem density and the level of competition in the stand. This may eventually produce unsatisfactory volume predictions at the stand level (Nunifu 2009). Sievanen (1993) stated that the ratio between the height and diameter is a function of the tree's ability to put on diameter growth. In support of this study, height–diameter relationships have ecological significance which is well documented in forestry literature (e.g., Opio et al. 2000; Meng et al. 2006). It is therefore important to develop models for black spruce in MGM that can predict diameter growth based on the basic knowledge of competition and relative allocation of stem growth to diameter and height. The compatible diameter growth in MGM is the growth allocation to diameter in relation to height growth. I examined the effect of climate and competition on the compatible diameter growth of black spruce in western Canada. Apart from exploring the diameter-height growth relationship, the diameter-volume growth relationship was also examined.

In Chapter number four, I examine the effect of reserving data on model performance and present results from validation of MGM for black spruce following application of the new submodels presented in the chapter three. MGM is an individual tree-based growth model that can project and evaluate stand growth and yield of important economic tree species for boreal forest which includes white spruce, black spruce, trembling aspen, lodgepole pine, jack pine and mixedwood stands in Alberta, British Columbia, Saskatchewan, and Manitoba (Bokalo 2012; Bokalo et al. 2013). Stand growth models like MGM have been developed to assist decision makers in estimating growth and yield outcomes for a range of management practices (Bokalo et al. 2013). It is important to assess performance of a model like MGM to ascertain the reliability of the model for forest management planning. Like most models, MGM can overestimate or underestimate stand variables (volume, basal area, average DBH, density etc) for a given species if conditions that influence growth and mortality of that species are not properly incorporated into the model. For instance, in a study on validation of MGM by Bokalo et al. 2013, the model effectively simulated juvenile and mature stages of stand development for both pure and mixed species stands of aspen and white spruce in Alberta but overestimated the increment in older stands which was likely due to the model failing to adequately account for age-related pathology and weather-related stand damage. Understanding MGM performance in black spruce growth and yield prediction is important in management planning. Validation is one aspect of the evaluation process that assesses the degree of accuracy attained by a model (Pretzch et al. 2002; Yang et al. 2004). While model validation has been widely discussed, there is little consensus on an acceptable approach (Bokalo et al. 2013) especially regarding the need of reserving data for validation. Data splitting is commonly used in model validation (Huang et al. 2003), although Kozak and Kozak (2003) suggested that it was an ineffective method and should be avoided. Furthermore, modelers have been advised to look for a more steady, consistent and repeatable approach towards the data used for validation (Huang et al. 2003), since data reserved for validation would have contributed to model performance. Therefore, it is necessary to evaluate the effect of data reservation on model performance i.e. using a smaller dataset and not the larger dataset for model fiitting. This is an important consideration when there is a small dataset since splitting it into two (calibration and validation) can have serious negative effects on the quality of the model. The objective of this part of my study was to provide information that will support forest modellers in making sound decisions for reserving data for validation.

Chapter 2: Release response of black spruce (*Picea mariana* (Mill.) B.S.P.) and white spruce (*Picea glauca* [Moench] Voss) following overstory lodgepole pine (*Pinus contorta* var. latifolia Engelm.) mortality due to mountain pine beetle attack.

2.1 Introduction

Mountain pine beetle, MPB (*Dendroctonus ponderosae* Hopkins) is an important natural disturbance agent in western North America. Its distribution is influenced by climate and forest type (Taylor et al. 2006). Following MPB outbreaks, there is a need to regenerate affected stands to meet forest management objectives. However, regenerating these affected stands to lodgepole pine forest will require silvicultural interventions due to issues related to (1) cone serotiny, and (2) lack of favourable seed bed for pine regeneration (McIntosh and Macdonald 2013). Fire or anthrogenic disturbance is often required to obtain acceptable amounts of lodgepole pine regeneration (Teste et al. 2011). Silvicultural interventions including planting seedlings, site preparation and salvage harvesting are expensive and have ecological issues (Dhar and Hawkins 2011).

Salvage harvesting following MPB infestation may have negative impacts on watershed function and aquatic habitat (Redding et al. 2008) and such impacts can be reduced when salvage logging is avoided (Dhar et al. 2016a) or only practiced on a portion of the landscape. Unsalvaged stands are important for wildlife habitat and biodiversity conservation (Chan-McLeod 2006; Dhar et al. 2016b). Natural disturbances like MPB are seen by many ecologists as an important ecological process rather than as an ecological disaster requiring human restoration (Lindenmayer et al. 2004) and these disturbances have been linked to maintenance of biodiversity and productivity (Bradstock et al. 2002).

Furthermore, since MPB induced mortality emulates a thinning from above, it should allow surviving trees to immediately take advantage of increased resources (water, nutrient, light) (Hawkins et al. 2013). Advance regeneration in affected stands can form a continuous new canopy and contribute significantly to stand recovery in stands affected by MPB outbreaks (Campbell and Antos 2015) by improving ecological processes and hydrologic recovery of the forest (Dhar and Hawkins 2011). This layer is generally dominated by shade tolerant species such as Engelmann spruce (*Picea engelmannii* Parry), white spruce (*Picea glauca* [Moench] Voss), hybrid (interior) spruce (*Picea glauca* [Moench] Voss x *engelmannii* Parry ex Engelm.), black spruce (*Picea mariana* (Mill.) B.S.P.), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) which are capable of surviving under reduced light levels common in the understory of lodgepole pine stands (Hawkins et al. 2012). Quantifying the growth of these residual trees is important for predicting the long-term potential of these stands and for selecting stands which require silvicultural interventions to improve growth and yield (Dhar and Hawkins 2011). Since it is not known how white spruce and black spruce will respond after MPB attack in Alberta research is needed to quantify the growth of the spruce advance regeneration to support management decisions and modelling.

Previous studies have shown that release response of spruce is influenced by site productivity, size of trees at release, condition of trees (and damage) following release, and amount of overtopping conifer and deciduous (DeRose and Long 2010). As a result, strong release responses (i.e., large growth increases) have been observed for shade-tolerant species, such as spruce and subalpine fir, following canopy opening (Hawkins et al. 2013) and even after prolonged suppression (Antos et al., 2000). The release that occurs following the sudden death of canopy trees following MPB outbreaks, has been observed to be more rapid and prolonged than that following the slow death of canopy trees, such as death caused by root diseases (Thompson et al. 2007). The inherent complexity of advance regeneration (in species abundance or composition, spatial distribution, range of sizes, development, health, and degree of release) and the scale of the current MPB infestation may significantly limit the use of simple empirical models (Kimmins et al. 2005) for predicting stand growth and yield. Therefore, the need to calibrate growth models such as the Mixedwood Growth Model (MGM) for this condition cannot be overemphasized. To support the issue of complexity of advance growth responses, significant release responses in advance regeneration were seen in smaller trees (Claveau et al. 2002), larger trees (Webb and Scanga 2001), younger trees (Helms and Standiford 1985; Hawkins et al. 2013), or without any age or size dependence (Puttonen and Vyse 1998). Understanding factors that contribute to variation in release responses for black and white spruce could be useful to improve our ability to predict stand growth for these conditions.

Commonly reported morphological indicators of growth response of advance regeneration are age, pre-release height growth, height, live-crown ratio, stem height/ diameter ratio, and logging damage (Ruel et al. 2000). Trees generally increase allocation of photosynthate to radial and height growth due to increases in resources including light, nutrients, water, and space. However, trees regulate the amount of photosynthate allocated to either diameter or height growth as a way to improve stability against windthrow (Meng et al. 2006). Both diameter and height growth are sensitive to environmental changes with priority depending on species, as well as pre- and post-release conditions (Gavrikov and Sebtenko 1996; Duchesneau et al. 2000).

As MPB results in death of overstory pines, one important stand characteristics that is expected to be affected drastically is understory light levels (Coates and Hall 2005). Light is a major requirement for understory growth and natural regeneration of lodgepole pine (Dhar et al. 2016a). Studies have revealed low light levels in the understory for a long period of time after MPB outbreaks (Coates and Hall 2005). Since stand structure and residual stand characteristics after MPB outbreaks differ between sites, it is important to understand how stand conditions will influence understory light levels following MPB outbreaks.

The objectives of the study were to:

1. Examine changes in diameter and height growth of black spruce and white spruce associated with MPB. The following questions were addressed:
   a) were there changes in spruce tree growth after overstory release? ; and,
   b) do white spruce and black spruce respond to release in the same way?
2. Examine how dead tree density, live pine density, and spruce/fir density will affect understory light. Specifically the following were addressed:
   a) evaluate the effects of plot assessment radius; and
   b) explore the utility of various competition indices for estimating understory light.
3. Examine whether diameter and height growth responses are related to their initial sizes, live pine tree density, dead tree density, spruce/fir tree density and age?

2.2 Materials and Methods

2.2.1 Study area

The study area was located in the Lower Foothills natural subregion of Alberta (Figure 2.1). For this study, I selected seven lodgepole pine dominated permanent sample plots (PSPs) (Alberta Sustainable Resource Development; ASRD 2005) with black and white spruce advance regeneration that were attacked by MPB in 2007-2008 but left unharvested. Five of these stands located south of Grand Prairie (GP) had high pine mortality while the other two stands located near Whitecourt (WC) had low pine mortality (Table 2.1 and Figure 2.1). Fieldwork was completed in the summers of 2015 and 2016.

Table 2.1 Selected plots coordinates.

Plot	Latitude	Longitude	Elevation	MAT	MAP
GP1	54.638	118.974	1041.806	2.9	628
GP2	54.670	118.993	1056.537	2.9	633
GP3	54.686	118.982	994.735	2.9	621
GP4	54.720	118.952	990.97	2.8	616
GP5	54.557	118.682	955.735	2.8	605
WC1	54.298	116.442	963.788	2.7	606
WC2	54.324	116.249	977.796	2.8	620

GP-Grand Prairie (high mortality plots) ; WC- Whitecourt (low mortality plots); MAT- mean annual temperature, MAP- mean annual precipitation; climate data extracted from "1981-2010 NA Climate Normals" for each plot, available at https://sites.ualberta.ca/~ahamann/data/climatewna.html, accessed on April 10th, 2018.

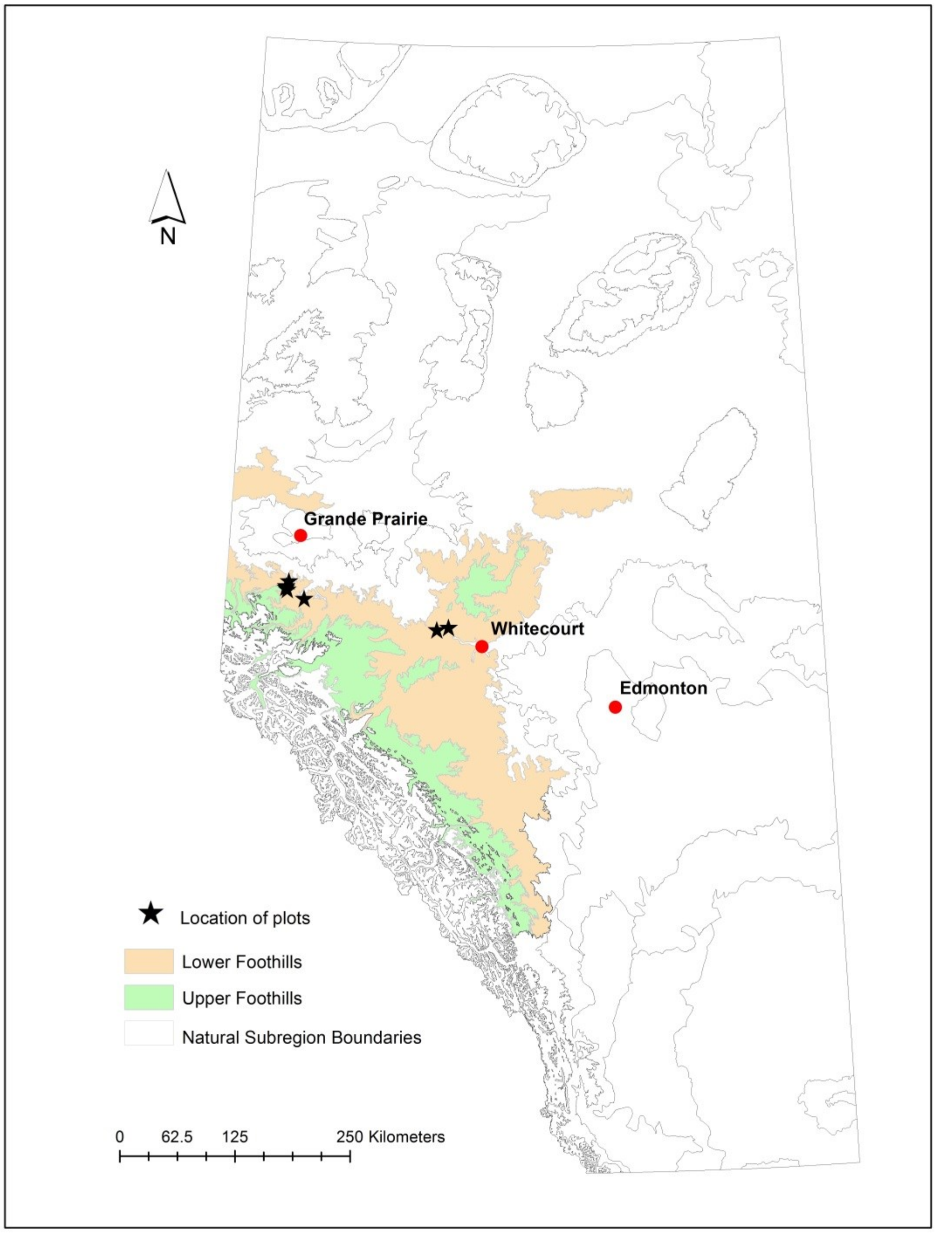

Figure 2.1 Location of sample plots. All plots were within the Lower Foothills Natural Subregion, which lies within the Foothills Natural Region of Alberta, Canada.

2.2.2 Data collection

In each of the five plots with high pine mortality, 24 black spruce and 24 white spruce trees were selected while in the low mortality plots, 20 black spruce and 20 white spruce were selected. These trees were selected to represent the range of variation in understory spruce densities and height (above 1.3m in height) within each stand. In a 5.64 m radius plot, centered on the sample tree, diameter at breast height (DBH) and height of all trees taller than 1.3 m were measured as well as their distances from the sample tree. A smaller competition plot (3.99m) within the already established 5.64m plot was also established. All trees taller than 1.3 m were also measured.

Table 2.2 summarizes data collected in all sampled plots. Each sample tree was harvested and height increments for each of the preceding 15 years were determined using budscars and branch whorls. Stem diameter was also recorded at 30 cm and 130 cm height and disks were also taken from 30 cm and 130 cm height for measurement of radial increment. These collected disks were measured for diameter outside bark and then air dried and sanded. Ring widths from pith to bark were measured in the lab to a precision of 0.001 mm along 4 radii separated by 90° using the WinDendro computer program and a calibrated scanner (Regent Instruments Canada Inc, 2009). After trees were felled, a hemispherical photograph was taken using a Nikon D90 camera fitted with a Sigma 4.5mm circular fisheye lens at 1.0 m height above the ground. Photos were taken either early in the morning or late in the evening when the sun was not visible above the horizon. Photos were processed using SLIM (Spot Light Interception Model) software (Comeau et al. 2003) to estimate the influence of the surrounding stand on light levels (fractional transmittance) at the sampled tree. Estimates of percent (%) transmittance from SLIM were used in this study.

Table 2.2 Mean diameter, height and height-diameter ratio (H/D) of white spruce (Sw) and black spruce (Sb) for each plot (values in parenthesis are sample standard deviation).

Mortality	Plot	Species	DBH(cm)	Height(m)	H/D ratio
High	GP1	Sb	8.98 (4.18)	7.54 (3.00)	0.89 (0.24)
		Sw	8.22 (4.26)	6.43 (3.13)	0.84 (0.16)
	GP2	Sb	9.02 (3.36)	7.21 (2.11)	0.83 (0.13)
		Sw	7.95 (3.97)	6.37 (3.22)	0.81 (0.11)
	GP3	Sb	10.27 (4.22)	9.49 (2.96)	0.87 (0.11)
		Sw	10.10 (4.51)	8.69 (3.55)	0.88 (0.11)
	GP4	Sb	7.80 (4.15)	6.38 (2.27)	0.82 (0.19)
		Sw	8.57 (4.68)	5.98 (3.34)	0.72 (0.14)
	GP5	Sb	10.42 (3.67)	9.08 (2.95)	0.89 (0.14)
		Sw	9.58 (4.25)	8.09 (3.67)	0.85 (0.11)
Low	WC1	Sb	5.84 (3.68)	5.20 (2.67)	0.98 (0.21)
		Sw	9.53 (5.33)	7.42 (4.04)	0.81 (0.12)
	WC2	Sb	6.82 (4.05)	6.31 (3.50)	0.98 (0.22)
		Sw	10.14 (3.67)	8.64 (3.22)	0.87 (0.10)

GP-Grand Prairie (high mortality plots) ; WC- Whitecourt (low mortality plots)

2.2.3 Data analysis

2.2.3.1 Release response of spruce across pre and post-MPB periods

Diameter increment and height increments measured over the three years before release (2004- 2006) and over the seven years after release (2008- 2014) were selected for comparison. A mixed model analysis of variance (ANOVA) was used to test the hypothesis that there was no difference between pre and post-release growth rates across the selected years. Tukey's honest significant difference (HSD) test was used to compare differences among years by comparing least square means (lsmeans) (Lenth 2016). Diagnostic plots of residuals versus fitted values were used to ascertain model fit. Random effects were included to account for variation among plots. Only the high mortality plots were used in this analysis because of the negative growth associated with one of the low mortality plots (Plot WC2) which is likely due to increases in soil water after MPB (Figure 2.2). Two models fit for each of white and black spruce, one for diameter and one for height resulting in a total of four models. The statistical model is:

[Eq. 2.1] $\mathrm{Y}_{ijk} = \mu + \mathrm{Year}_k + \mathrm{Plot}_i + \mathrm{Tree}_{j(i)} + \varepsilon_{ijk}$,

where $\mathrm{Y}_{\mathrm{ijk}}$ is diameter and height increment , $\mathrm{Year}_{\mathrm{k}}$ is the fixed effect for years, $\mathrm{Plot}_{\mathrm{i}}$ is the random effect for plot, $\mathrm{Tree}_{j(i)}$ is the random effect for tree nested within plot and $\varepsilon_{\mathrm{ijk}}$ is the random experimental error.

2.2.3.2 Understory light

Understory light is often related to densities of neighboring trees and as such various stand densities estimators have been used as predictor variables in understory light models (Comeau and Heineman 2003; Lochhead and Comeau 2012). Basal area is widely used as a measure of density and competition (Contreras et al. 2011; Huang et al. 2013) and it is reported to be more accurate than using number of stems per hectare since it captures both the number of trees in a stand and their sizes (Zeide 2005).

In this study, total basal area was estimated as the basal area per hectare of all trees irrespective of status (dead or alive). Dead and live pine basal area were estimated as the total basal area per hectare of dead (killed by MPB) and live lodgepole pine trees within the 5.64m competition plot, respectively. Spruce/fir basal area was estimated as the total basal area of spruce/fir trees within the 5.64m competition plot. Release intensity (impact of pine mortality) was estimated following Puettmann and Saunders (2000) as the percentage of lodgepole pine trees in the 5.64m radius competition plot killed by MPB.

[Eq. 2.2] $$\text{Release intensity (RI, \%)} = \frac{\text{Dead tree basal area}}{\text{Total basal area}}\, X\ 100$$

A linear mixed effect model was developed to examine the relationship between understory light and stand variables including live pine basal area, release intensity, and spruce/fir basal area. The understory light captured in this study was the total light over the growing season expressed as % if open sky values and it was used as the response variable as presented in the model below;

[Eq. 2.3] $$\text{Total light}_{\text{ij}} = (\beta_0 + \text{b}_\text{i}) + \beta_1\text{Live pine tree}_{\text{ij}} + \beta_2\text{Spruce/fir tree}_{\text{ij}} + \beta_3\text{Release intensity}_{\text{ij}} + \varepsilon_{\text{ij}}$$

where $\text{Total light}_{\text{ij}}$ is the j^{th} light observation within Plot_i. β_0 is the intercept. β_1 , β_2 and β_3 are coefficients to be estimated. b_i is the random effect associated with $Plot_i$, and ε_{ij} is the random error.

To further examine the effect of spruce/fir competition on understory light, three competition indices were estimated for spruce/fir tree density (Table 2.3). They include distance dependent (CI 1a and CI 1b) and distance independent competition indices (C1 2a, CI 2b, CI 3a and CI 3b). The effect of assessment plot radius (3.99m or 5.64m) was also tested. The competition indices as presented in Table 2.3 include total basal area, basal area distance ratio which is a modification of the diameter distance ratio (Cortini and Comeau 2008) and Hegyi's index which is also a modification of the original Hegyi's formula (Hegyi 1974).

Table 2.3 Competition indices and formula used for their calculation.

Competition indices (CI)	Radius plot	Formula
CI 1 : BA total (Distance independent)	**CI 1a**: 5.64m **CI 1b**: 3.99m	$\sum_{i=1}^{n} BA_i$
C1 2 : Basal area distance ratio (Distance dependent)	**CI 2a**: 5.64m **CI 2b**: 3.99m	$\sum_{i=1}^{n} \frac{BA_i}{Distance_{ti}}$
CI 3 : Hegyi's (Distance dependent)	**CI 3a** : 5.64m **CI 3b** : 3.99m	$\sum_{i=1}^{n} \frac{BA_i}{BA_t * Distance_{ti}}$

BA_i = basal area of competitor spruce/fir; BA_t = basal area of sample tree (centered tree); $Distance_{ti}$ is distance between sample tree and competitor trees.

Several models were developed using the various competition indices and plot radii (Table 2.3). Comparison of models were carried out using coefficient of determination (R^2) and Aikake Information Criterion (AIC) values. The coefficient of determination (R^2) of the mixed effect models were estimated by using the package MuMIn (Nakagawa and Schielzeth 2013; Bartón 2015). All statistical analysis was done in R environment (R Core Team 2015).

2.2.3.3 Effect of stand densities, age and initial tree size on growth responses of spruce following MPB outbreak

Covariates for analysis: Stand variables examined were live tree basal area, dead tree basal area, and spruce/fir competition while tree variables include initial tree size and age of sample tree. Initial testing indicated that spruce/fir basal area assessed within a 5.64 m radius plot was not significant in models describing variation in growth of either spruce species. Consequently, spruce/fir competition was estimated using basal area distance ratio which is a distance dependent competition index (CI2) shown in Table 2.3 (Cortini and Comeau 2008). CI2 was calculated using data for the 5.64m radius ($100m^2$) plots. Incorporating initial tree size into this study is supported by numerous studies that found initial size to greatly affect growth of released stems (Ferguson and Adams 1980; Gillespie and Hocker 1986; Filipescu and Comeau 2007). From the disk collected at breast height (130cm), the age of the tree at breast height was estimated as the number of counted rings. Initial size was the tree diameter or height one year prior to the year of attack.

Selection of response variable: Mean diameter increment and mean height increment (PAI) for 2012, 2013 and 2014 were used to estimate the diameter and height growth rate after release, respectively, while pre-release diameter and height growth were the mean diameter and mean height increment for 2004, 2005 and 2006. Preliminary exploration of data (Figures 2 and 3) indicates that post-release growth (PAI) was related to prelease growth (PAI). Factors affecting pre-release growth were also examined in this study. The release response (growth ratio) was estimated as the ratio of post-release mean diameter increment (PAI_r) to pre-release mean diameter increment (PAI_u) for diameter growth ratio while height growth ratio was estimated as post-release mean height increment (PAI_r) to pre-release mean height increment (PAI_u) . The growth ratio captures how a tree respond following overstory lodgepole pine mortality in relation to its previous growth rates. It is related to the actual post-relase growth rates (except diameter growth for black spruce) (Figures 4 and 5). Similar estimation methods have been used as a response variable in other studies (Romme et al. 1986; Hawkins et al. 2013).

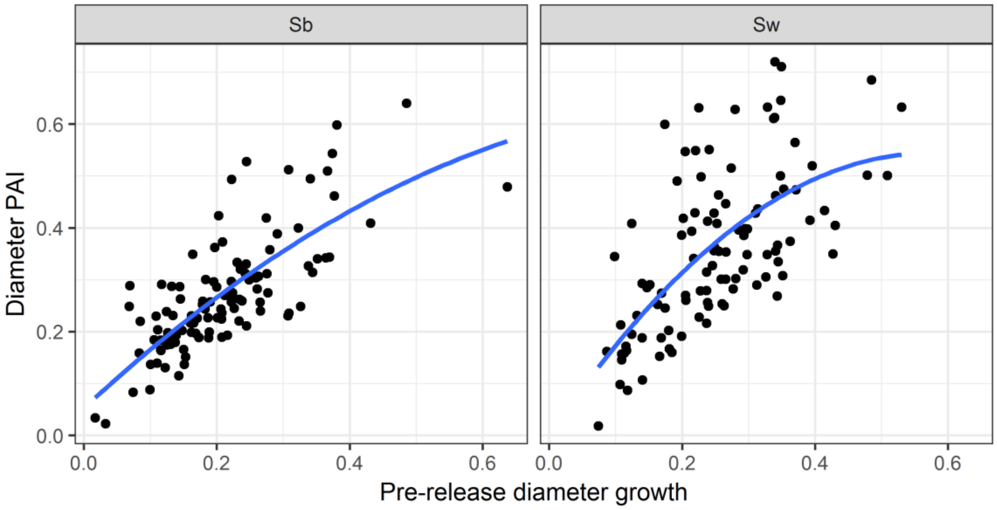

Figure 2.2 Relationship between post-release diameter growth (PAI) and pre-release diameter growth (PAI) for black spruce (Sb) and white spruce (Sw). Relationship was significant at $P < 0.05$ and models for both species were $y \sim x + x^2$. Sb (R^2=57.14) and Sw (R^2= 40.45).

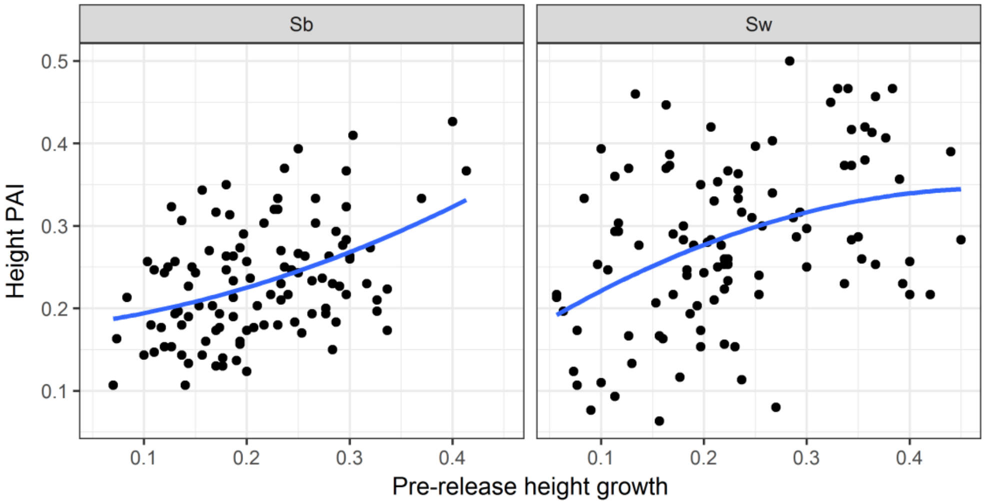

Figure 2.3 Relationship between post-release height growth (PAI) and pre-release height growth (PAI) for black spruce (Sb) and white spruce (Sw). Relationship was significant at P <0.05 and models for both species were y~x+x^2. Sb (R^2=28.19) and Sw (R^2= 25.99).

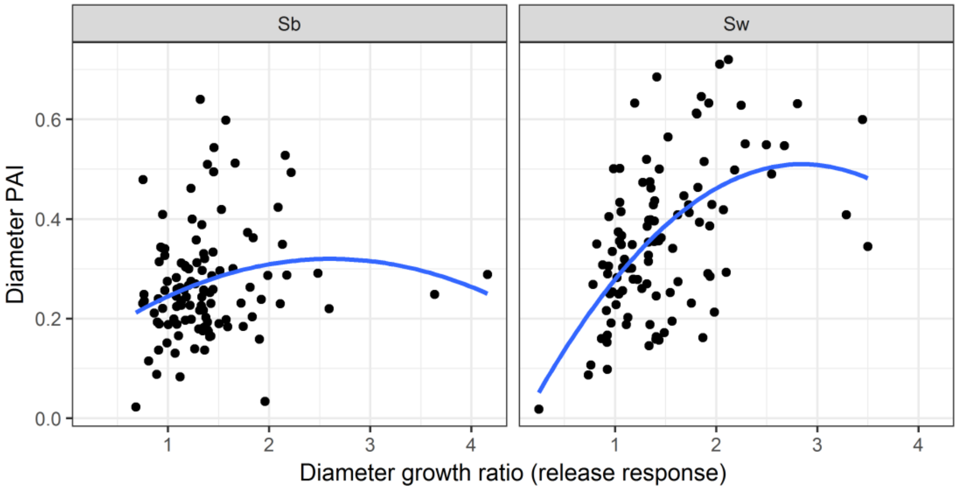

Figure 2.4 Relationship between post-release diameter growth (PAI) and diameter growth ratio (release response) for black spruce (Sb) and white spruce (Sw). Relationship was significant at P <0.05 for only Sw and models for both species were y~x+x^2. Sb (R^2=1.67) and Sw (R^2= 25.25).

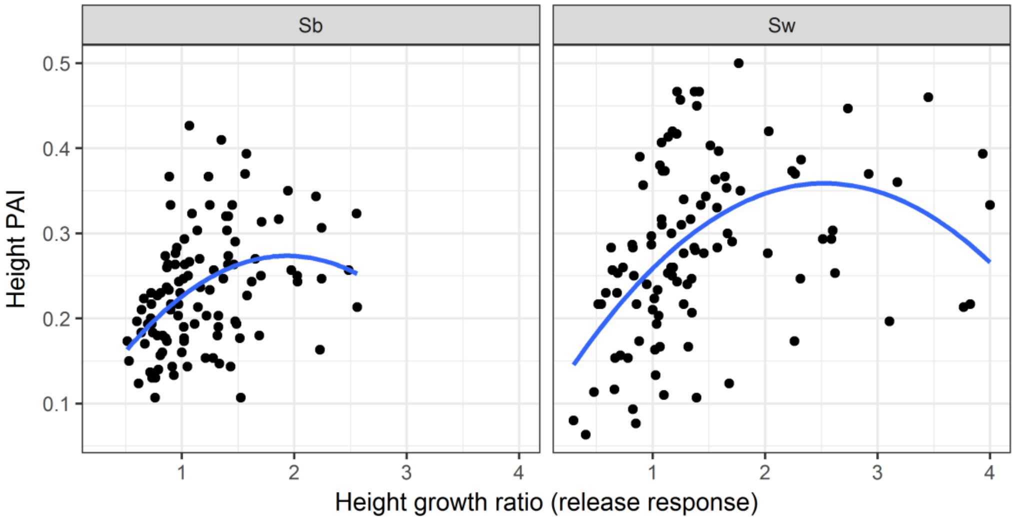

Figure 2.5 Relationship between post-release height growth (PAI) and height growth ratio (release response) for black spruce (Sb) and white spruce (Sw). Relationship was significant at P <0.05 and models for both species were $y \sim x + x^2$. Sb (R^2=12.50) and Sw (R^2= 10.06).

A non-linear mixed effect model was used to test for the effect of initial size, live tree density, spruce/fir competition and age on - (1) pre-release (PAI_u) and post-release (PAI_r) diameter growth rate (2) pre-release (PAI_u) and post-release (PAI_r) height growth rate and, (3) diameter and height growth ratio (release response). A random effect which is associated with plot was incorporated in the model. The analysis was done separately for white spruce and black spruce using only the high mortality plot data. The model form used was:

[Eq. 2.4] $$Y_{ij} = (\beta_0 + b_{0i}) * \exp^{((\beta_n * X_n))} + \varepsilon_{ij}$$

where Y_{ij} is the diameter or height growth rates, and release responses, β_0 and β_n are fixed parameters associated to be estimated. b_{0i} is the random effect associated with the plot, $X_n$is the tree and stand variables to be tested. n is the number of variables included in the model and ε_{ij} is the random error.

To avoid multicollinearity, variables with high correlation were not included in the same model (e.g dead tree basal area was removed from model because it was correlated with live pine tree basal area). This was done by removing variables with variance inflation factor (VIF) higher than 10 from the same model (Ma and Lei 2015). Variance functions were included to model heteroscedasticity (Pinheiro and Bates 2000).

2.3 Results

2.3.1 Stand characteristics

There were substantial differences in stand attributes between high and low mortality plots (Table 2.4). Plot GP2 had the highest dead tree basal area per hectare of 40.64 m^2/ha while the lowest was Plot WC1 (3.98 m^2/ha). Low mortality plots (WC1 and WC2) were less dense before attack (total basal area per hectare) than high mortality plots but have the highest live tree basal areas post-attack. The mean values of age, live and dead tree basal area as well as total basal area are shown in Table 2.4.

Table 2.4 Mean values for selected stand characteristics of sites sampled (Standard deviation in parenthesis).

Plot	Age (Years)		Live tree basal area(m^2/ha)	Dead tree basal area (m^2/ha)	Total Basal area (m^2/ha)
	Sb	Sw			
GP1	39.76(10.61)	36.05(9.29)	10.03 (8.55)	32.12 (11.33)	42.16 (12.21)
GP2	41.21(6.55)	35.00(9.63)	8.51 (5.73)	40.64 (15.21)	49.14 (17.06)
GP3	54.04(21.46)	43.08(7.15)	23.49 (14.06)	31.75 (14.23)	56.74 (13.74)
GP4	41.04(9.14)	35.13(9.48)	10.15 (7.33)	32.20 (15.36)	42.35 (17.64)
GP5	50.04(8.91)	46.08(6.44)	10.43 (7.63)	38.28 (13.74)	48.71 (12.40)
WC1	36.47(12.34)	45.25(22.21)	34.27 (13.42)	3.98 (3.85)	39.89 (14.29)
WC2	45.65(15.33)	114.05(33.03)	31.82 (12.06)	5.66 (6.16)	38.41 (11.19)

Sw- White spruce; Sb- Black spruce. Total Basal area (m^2/ha) is the summation of live and dead tree basal areas Total Basal area (m^2/ha).

Spruce diameter growth increased after MPB attack in six plots (Figure 2.2). However, increases in diameter growth were delayed for about four years in some plots, as observed in Plots GP1, GP2, GP3 and GP5 while a sharp increase was observed in the last two years (2013 and 2014). Growth after release differed between high mortality sites (Plots GP1, GP2, GP3, GP4 and GP5 and low mortality sites (Plots WC1 and WC2). For the low mortality plots: Plot WC1 continues to grow at a steady rate similar to prerelease growth (ie. pattern of growth before and after attack are similar) while Plot WC2 shows a decrease in growth after release.

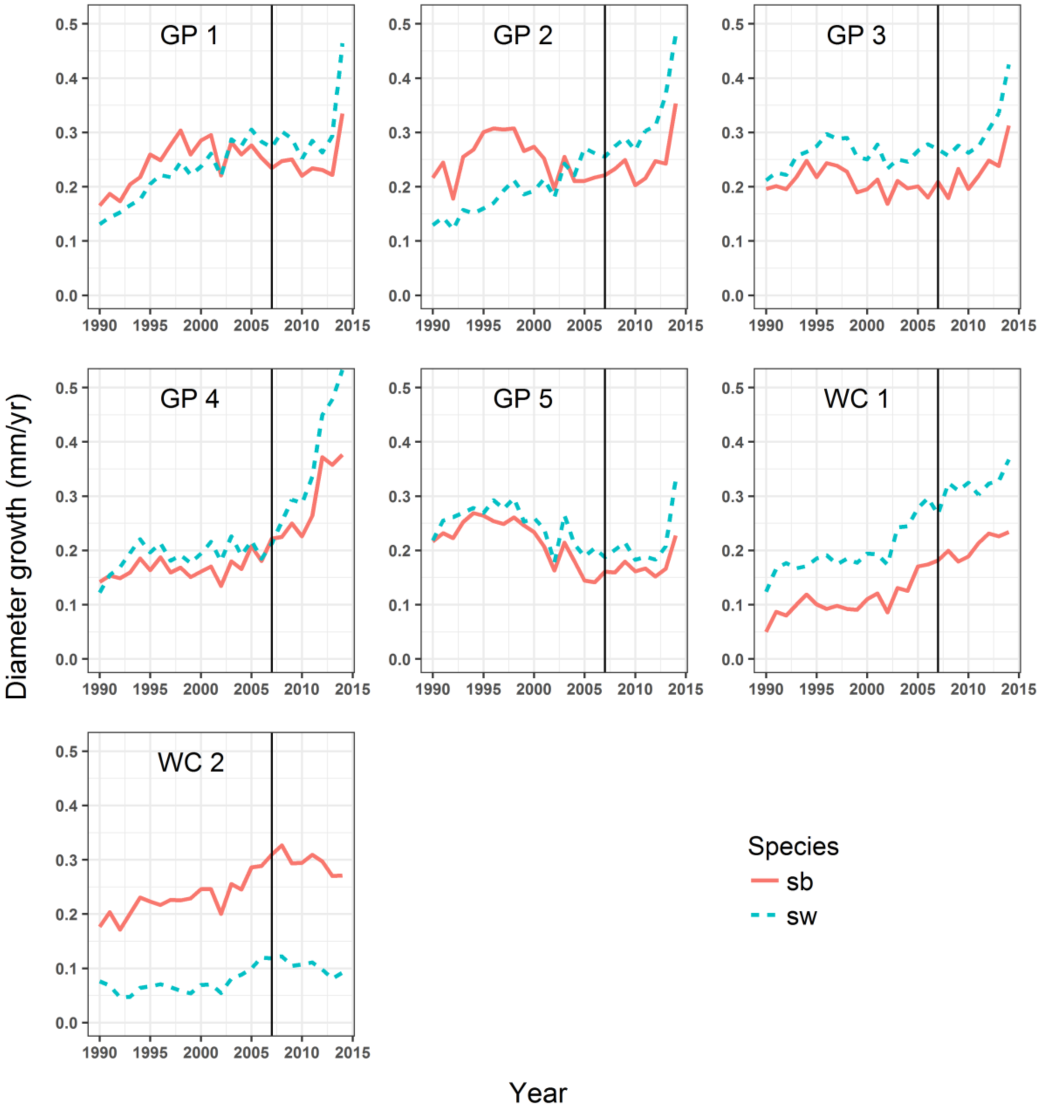

Figure 2.6 Mean diameter increment for sampled white (Sw) and black (Sb) spruce at each site by year, before and after MPB outbreak. Vertical line indicates time of release (year of MPB outbreak; 2007).

2.3.2 Diameter and height response of spruce following overstory lodgepole pine mortality

Since a delay in response (growth response time) was experienced in most of the plots, especially plots GP1, GP2, GP3, GP4 and GP5, it was necessary to examine the timing of delay averaged across plots.

2.3.2.1 Diameter growth response over time

Results from ANOVA showed a significant difference between years for white spruce (F= 47.49, P<0.0001) and black spruce (F= 35.68, P<0.0001). Figures 2.8 and 2.9 show diameter increment before and after release for white and black spruce, respectively. Results reveal a delayed response period for both species. White spruce responded significantly after 4 years while it took black spruce about 6 years to respond. The residual plots of the ANOVA models for diameter increment are displayed below (Figure 2.7) for both spruces.

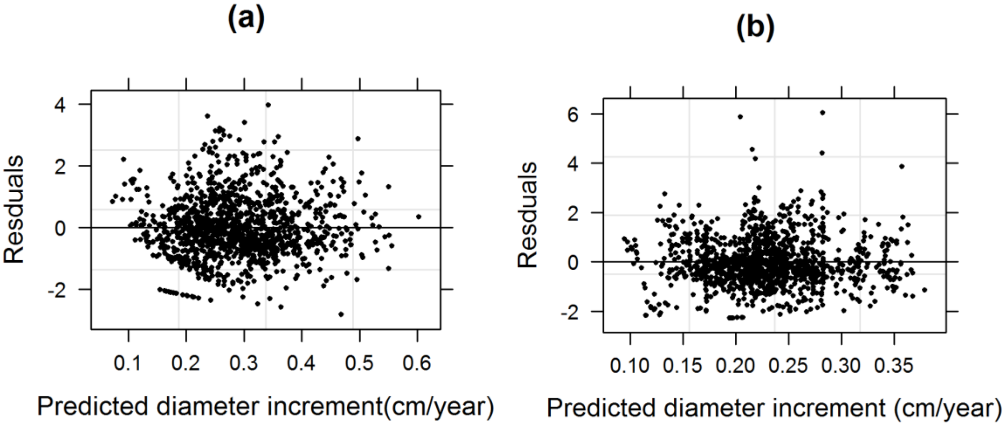

Figure 2.7 Residual plots of white spruce (a) and black spruce (b) diameter increment models.

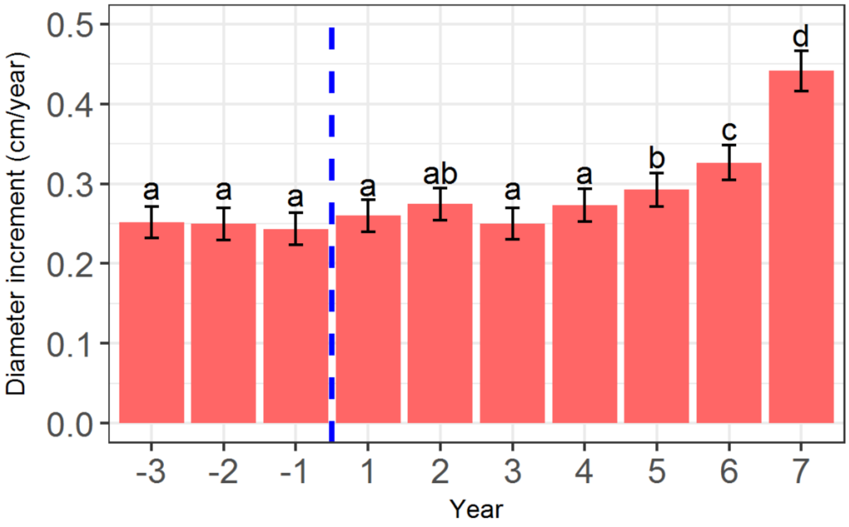

Figure 2.8 Barplot of LS means of diameter increment before and after release for white spruce (dashed line is the year of MPB attack). Different letters indicate significant difference between the years (P<0.05) and the error bars indicate the standard error.

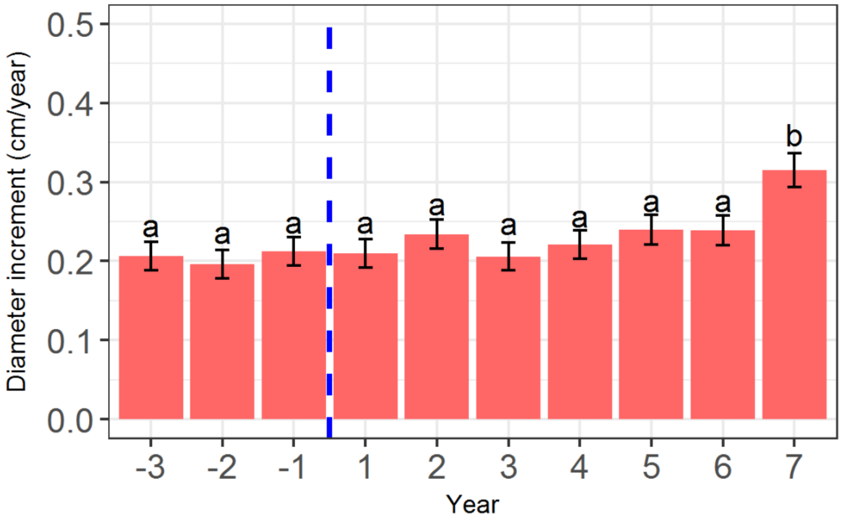

Figure 2.9 Barplot of LS means of diameter increment before and after release for black spruce (dashed line is the year of MPB attack). Different letters indicate significant difference between the years (P<0.05) and the error bars indicate the standard error.

2.3.2.2 Height growth response over time

Both white spruce and black spruce responded in height growth following MPB attack. Similar to diameter increment, white spruce responded earlier than black spruce (Figures 2.11 and 2.12). Results from the ANOVA model showed significant differences between height increment at various years for white spruce (F= 23.76, P<0.0001) and black spruce (F=20.63, P<0.0001) and the lsmeans are presented in Figure 2.11 for white spruce and Figure 2.12 for black spruce. White spruce responded in height after four years and black spruce responded after 5 years. The residual plots for the height increment models are shown in Figure 2.10 and indicate that the models have good fit.

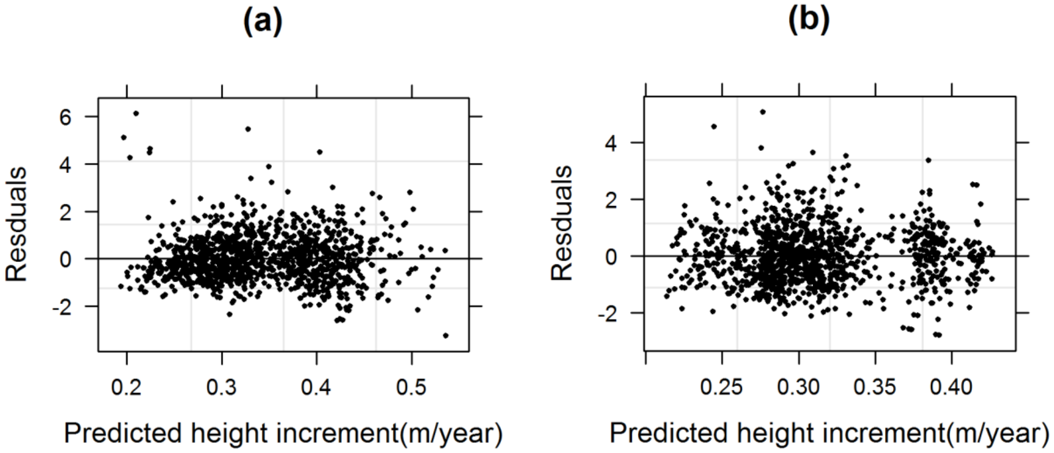

Figure 2.10 Residual plots of white (a) and black spruce (b) height increment models across pre and post-release periods.

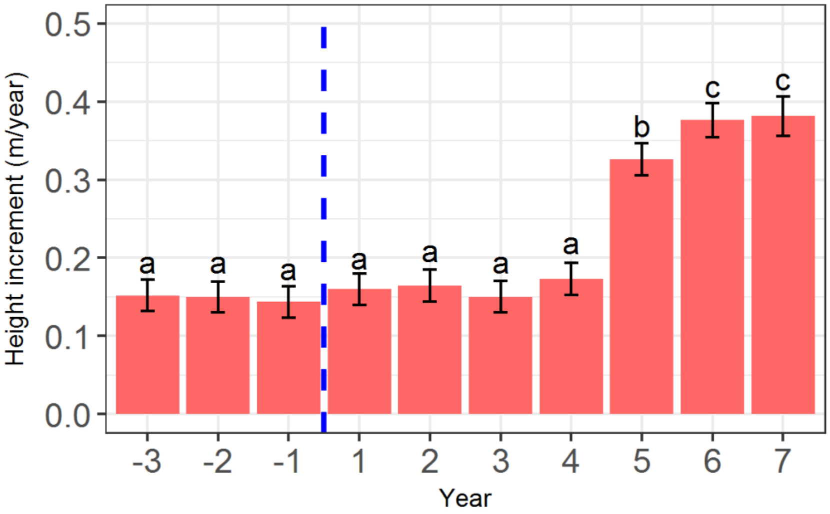

Figure 2.11 Barplot of LS means of height increment before and after release for white spruce (dashed line is the year of MPB attack). Different letters indicate significant differences between the years (P<0.05) and the error bars indicate the standard error.

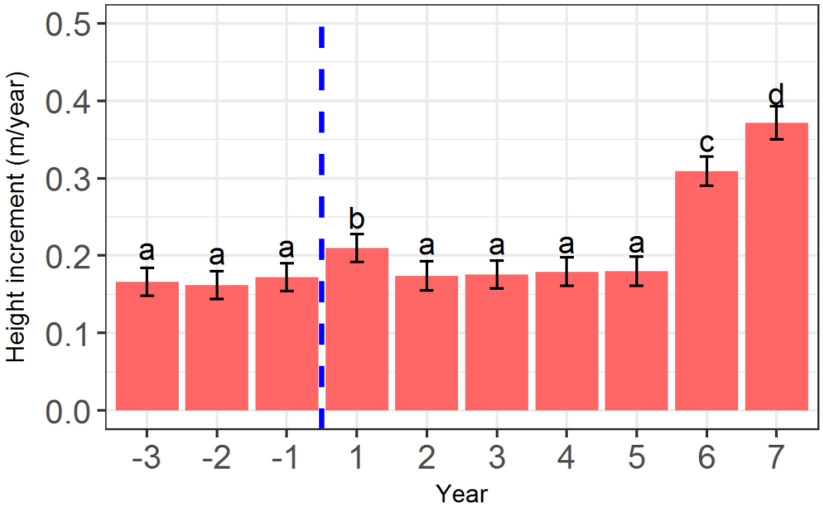

Figure 2.12 Barplot of LS means of height increment before and after release for black spruce (dashed line is the year of MPB attack). Different letters indicate significant differences between the years (P<0.05) and the error bars indicate the standard error.

2.3.3 Relationship between understory light following MPB outbreak and stand densities

Understory light was strongly affected by spruce/fir tree density but was not affected by live pine tree and release intensity (Table 2.5). Competition from spruce/fir trees showed a negative relationship on light. Though live tree and dead tree basal area were not significant, they showed a positive relationship to understory light. Power variance function (Pinheiro and Bates 2000) was included in the developed linear mixed model to model heteroscedasticity (Equation 2.5). The linear mixed effect model did not have any obvious biases as shown in the residual plot and the fitted versus observed understory light showed the model was slightly underpredicting understory light (Figure 2.13). Using the fixed effect components of the mixed model, the relationships between light and stand variables are displayed in Figure 2.14.

The developed model was:

[Eq. 2.5]

$$\text{Total light} =$$
$$\text{Intercept} + \text{Livepine basal area} + \text{Spruce/fir tree competition} + \text{Release intensity}$$

Table 2.5 Linear mixed effect model for understory light and competition variables (values in parenthesis are standard error of the estimate).

Parameter	**Estimate (SE)**	**p-value**
Intercept	53.413 (3.692)	0.0001
Live pine tree basal area	-0.038 (0.115)	0.6247
Spruce/fir tree competition (CI1a)	-14.551 (1.322)	**<0.0000***
Release intensity (%)	-0.038 (0.037)	0.4194

***significant at p<0.05**

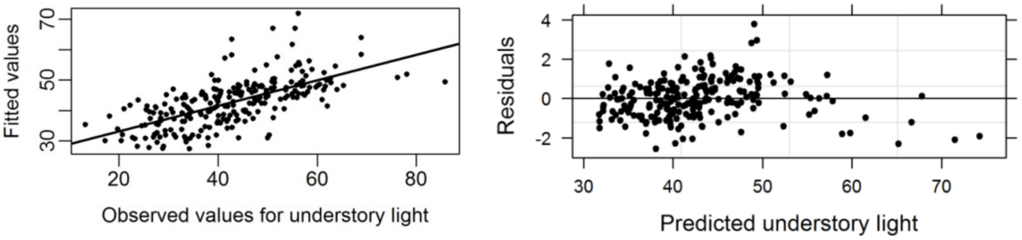

Figure 2.13 Plots of fitted and observed, and residuals for the understory light model.

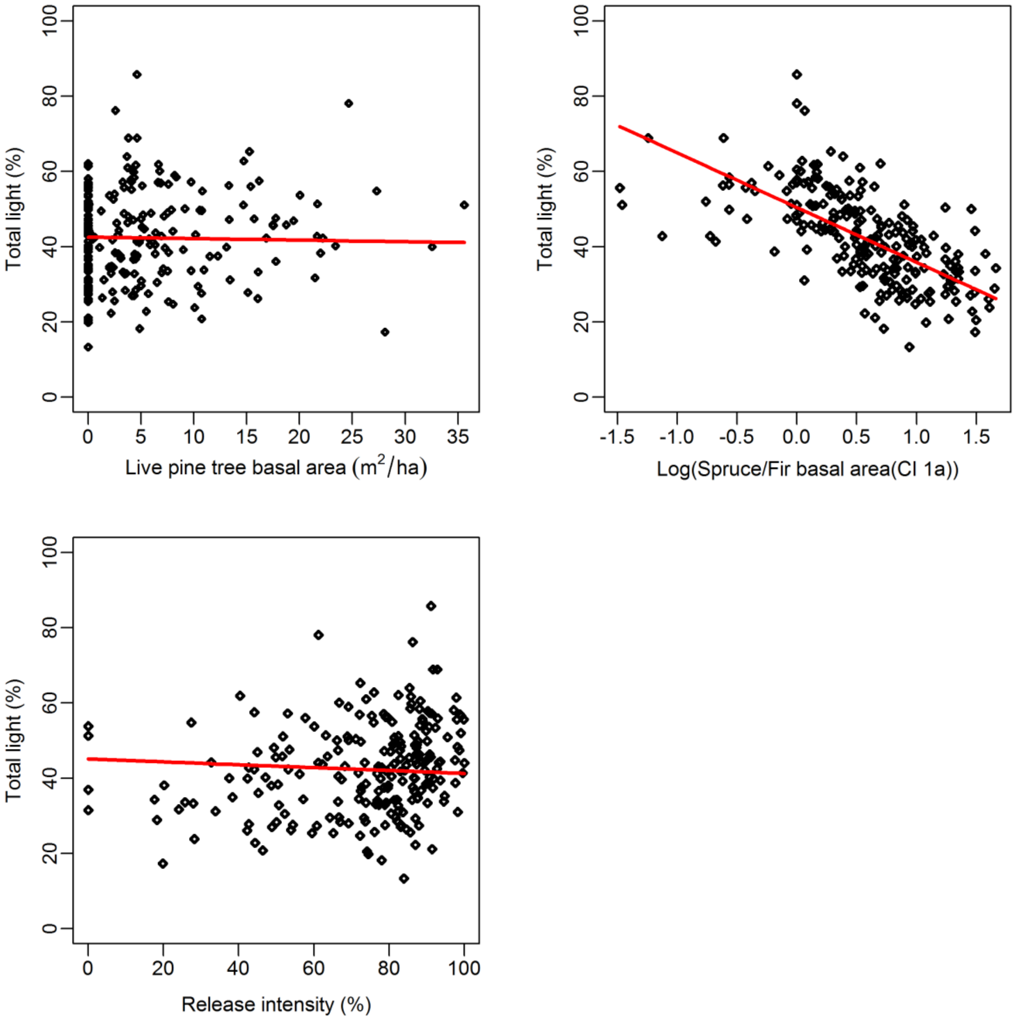

Figure 2.14 Relationships between total light and live pine tree and spruce/fir tree competition (CI 1a) and release intensity (%).

Since results from Table 2.5 show that only spruce/fir density has an impact on understory light, further examination of this effect using various spruce/fir tree competition indices (Table 2.3) resulted in the development of Equations 2.6 to 2.11, as showed below;

[Eq. 2.6] $Total\ light = Intercept + CI\ 1a$

[Eq. 2.7] $Total\ light = Intercept + CI\ 1b$

[Eq. 2.8] $Total\ light = Intercept + CI\ 2a$

[Eq. 2.9] $Total\ light = Intercept + CI\ 2b$

[Eq. 2.10] $Total\ light = Intercept + CI\ 3a$

[Eq. 2.11] $Total\ light = Intercept + CI\ 3b$

All the models were linear mixed models with plot as a random effect and a random slope for the competition indices. The best predictor of light among the three competition indices was the CI 2 (basal area distance ratio) followed by CI 1 (total basal area). Spruce/fir tree competition measured within 5.64m radius was better than 3.99m radius. For instance, the model fitted using CI 1a is better than CI 1b, while CI 2a is better than CI 2b and CI 3a is better than CI 3b (Table 2.6). The overall best model is Equation 2.8 (R^2=0.704), which is spruce/fir competition (5.64m radius) estimated using basal area distance ratio as the competition index. The R^2 values displayed in Table 2.6 were consistent with the AIC values.

Table 2.6 Linear mixed effect model for understory light and spruce/fir competition indices (values in parenthesis are standard error of the estimate).

Equation	Intercept	Predictor	AIC	Δ AIC	R^2
2.6	49.888 (4.930)	-13.837 (1.246)	1500.971	13.942	0.613
2.7	44.027 (6.629)	-10.947 (1.190)	1520.524	34.466	0.519
2.8	12.544 (6.267)	-15.285 (1.165)	**1486.058**	**0**	**0.704**
2.9	16.316 (7.016)	-11.778 (0.876)	1515.391	29.333	0.564
2.10	49.926 (5.945)	-16.502 (1.658)	1520.413	34.355	0.498
2.11	45.998 (6.217)	-12.754 (1.596)	1534.458	48.400	0.437

Figure 2.15 illustrates how well the various models predict observed values. The Hegyi's competition index using 3.99m radius (CI 3b) was the weakest model (Figure 2.15f). The points are far from the fitted line and there is also under prediction. The best model (Figure 2.15c) had points which were closer to the fitted line and under prediction was reduced.

The relationship between total light and all competition indices as predicted by the models are illustrated in Figure 2.16.

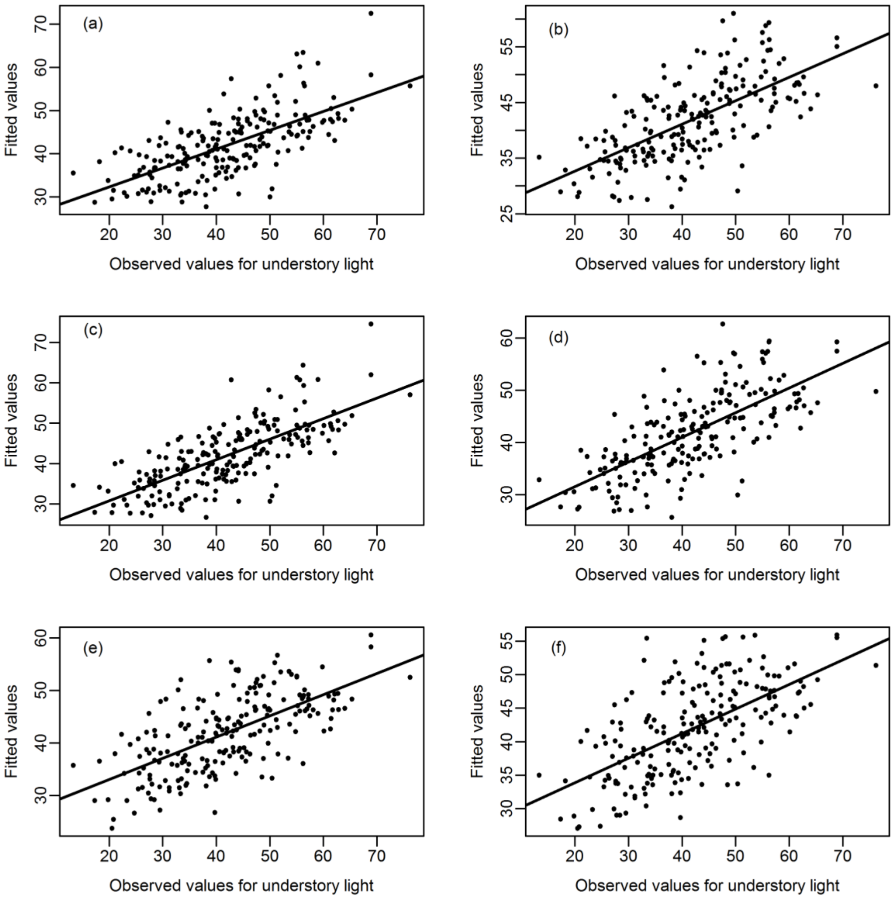

Figure 2.15 Fitted and observed plots for all spruce/fir tree competition indices (Eqn 2.6(a); Eqn.2.7(b); Eqn 2.8(c); Eqn 2.9(d); Eqn 2.10(e) ; Eqn 2.11(f)).

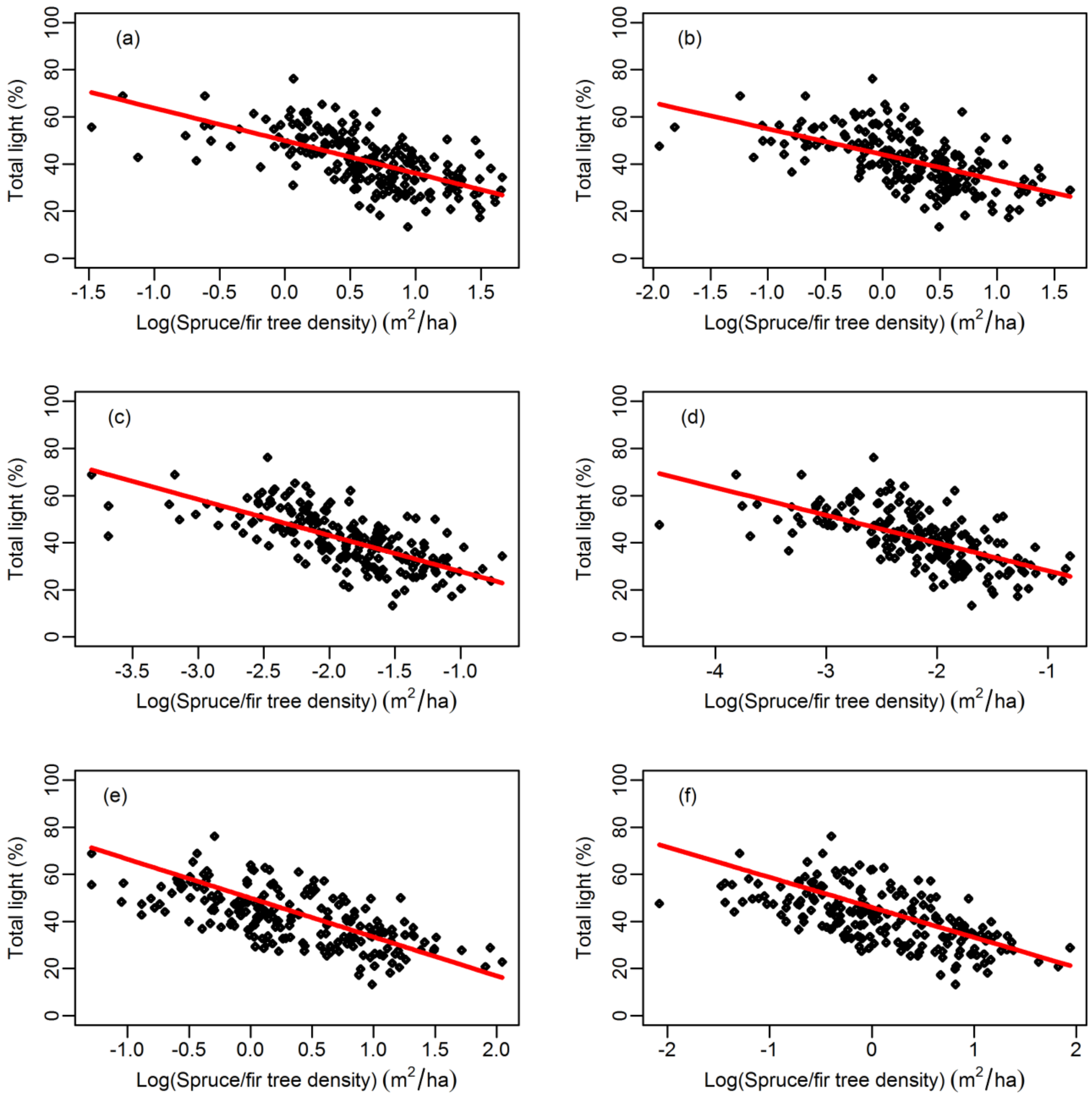

Figure 2.16 Relationship between total light and spruce/fir competition indices (Eqn 2.8(a); Eqn.2.9(b); Eqn 2.10(c); Eqn 2.11(d); Eqn 2.12(e) ; Eqn 2.13(f)). The best model is Eqn 2.10(c).

2.3.4 Effect of tree and stand conditions on pre and post-release diameter growth rate

The nonlinear mixed effect model developed for diameter growth response (pre and post) included initial DBH, live tree basal area, spruce/fir competition (CI2) and age. A power variance function (Pinheiro and Bates 2000) was included for diameter growth. A plot level random effect was also incorporated in the model to capture variation among plots.

The developed diameter growth model is:

[Eq. 2.12]

$$Y_{ijk} = (\beta_0 + b_{0i}) * \exp^{(((\beta_1 \text{ Initial dbh} + \beta_2 \text{ Live tree basal area} + \beta_3 \text{Spruce/fir competition} + \beta_4 \text{ Age})))} + \varepsilon_{ijk}$$

2.3.4.1 Pre-release diameter growth rate

The relationship between pre-release growth rate and tree and stand variables are shown in Table 2.7. Initial DBH of both spruces was significantly related to pre-release growth. Both showed a positive relationship. On the other hand, age of both species was negatively related to pre-release growth. Estimates of parameters also reveal that live tree basal area was not related to pre-release growth for either species (Table 2.7). The simplified model showing only significant variables (Table 2.8) revealed that white spruce was negatively affected by spruce/fir competition but spruce/fir competition did not show any effect on black spruce. The residual plots and fitted versus observed plots of the pre-release diameter growth model (Table 2.7) for both spruces are shown in Figures 2.17 and 2.18 respectively.

2.3.4.2 Post-release diameter growth rate

Post-release growth was significantly affected by initial DBH, spruce/fir competition and age. Similar to the pre-release diameter growth, initial DBH and age affected post-release growth positively and negatively, respectively. The higher the spruce/fir competition, the lower the post-release growth of both spruces. No effect of live pine tree basal area was observed for either spruce species (Table 2.7 and 2.8). The residual plots and fitted versus observed plots of the post-release diameter growth model for both spruces are shown in Figures 2.17 and 2.18 respectively.

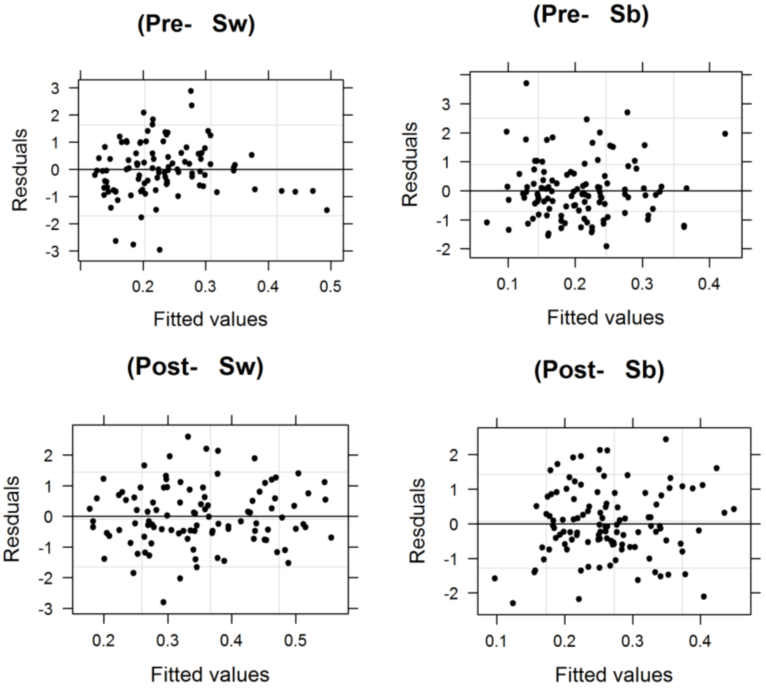

Figure 2.17 Residuals for pre and post –release diameter growth models for white spruce and black spruce.

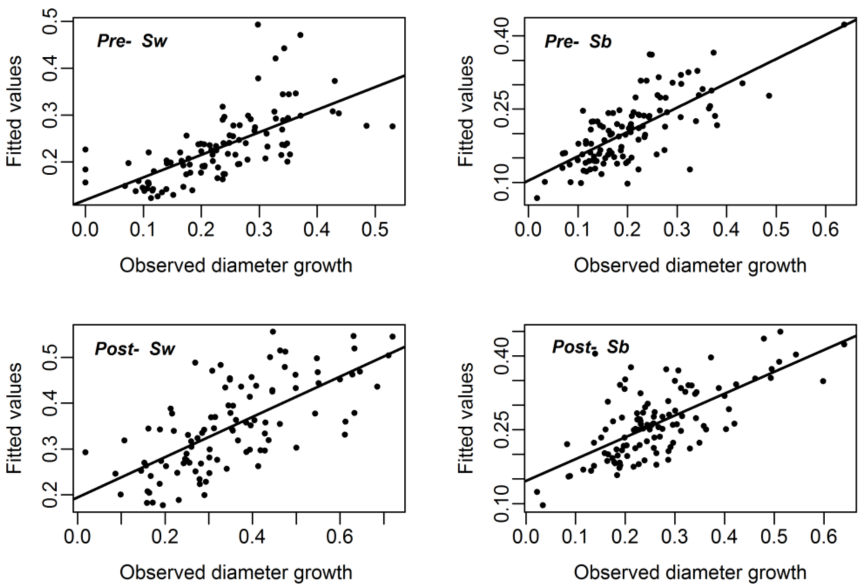

Figure 2.18 Plots of fitted versus observed values for pre and post-release diameter growth for white spruce and black spruce.

Table 2.7 Mixed effects models for pre-release and post release diameter growth of white and black spruce fitted with selected variables (values in parenthesis are standard error of the estimate).

	Pre- release growth rate				**Post- release growth rate**			
Variable	**White spruce**		**Black spruce**		**White spruce**		**Black spruce**	
	Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value
Intercept	0.2701 (0.044)	**0.0001**	0.4519 (0.060)	**<0.0001**	0.4955 (0.086)	**0.0001**	0.4355 (0.070)	**<0.0001**
Initial dbh	0.1166 (0.012)	**0.0003***	0.1311 (0.016)	**<0.0001***	0.0732 (0.016)	**0.0001***	0.0885 (0.014)	**<0.0001***
Live pine tree basal area	-0.0189 (0.005)	0.1727	-0.0161 (0.004)	0.1007	-0.0069 (0.006)	0.2711	0.0108 (0.005)	0.0514
Spruce/fir competition (CI2)	-0.1339 (0.006)	0.0537	-0.0368 (0.066)	0.5790	-0.1704 (0.068)	**0.0142***	-0.1278 (0.067)	**0.0401***
Age	-0.0215 (0.005)	**0.0036***	-0.0475 (0.006)	**<0.0001***	-0.0199 (0.007)	**0.0046***	-0.0287 (0.005)	**0.0001***

***significant at $p<0.05$**

Table 2.8 Simplified mixed effects models for pre-release and post release diameter growth of white and black spruce with only significant variables (values in parenthesis are standard error of the estimate).

	Pre- release growth rate				**Post- release growth rate**			
Variable	**White spruce**		**Black spruce**		**White spruce**		**Black spruce**	
	Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value
Intercept	0.2912 (0.011)	**0.0001**	0.4409 (0.033)	**0.0012**	0.3782 (0.077)	**0.0001**	0.4355 (0.070)	**<0.0001**
Initial dbh	0.1055 (0.008)	**0.0001***	0.1321 (0.014)	**0.0009***	0.0790 (0.010)	**0.0001***	0.0885 (0.014)	**<0.0001***
Live pine tree basal area	ns		ns		ns		ns	
Spruce/fir competition (CI2)	-0.1809 (0.012)	**0.0322***	ns		-0.1864 (0.025)	**0.0142***	-0.1278 (0.067)	**0.0401***
Age	-0.0204 (0.001)	**0.0079***	-0.0535 (0.016)	**<0.0001***	-0.0221 (0.002)	**0.0046***	-0.0287 (0.005)	**0.0001***

***significant at p<0.05**

The relationship between post-release growth and initial size, age, live pine tree and spruce/fir competition are further illustrated using the model estimates (Figure 2.19). In general, the mean growth rate of white spruce was higher than black spruce.

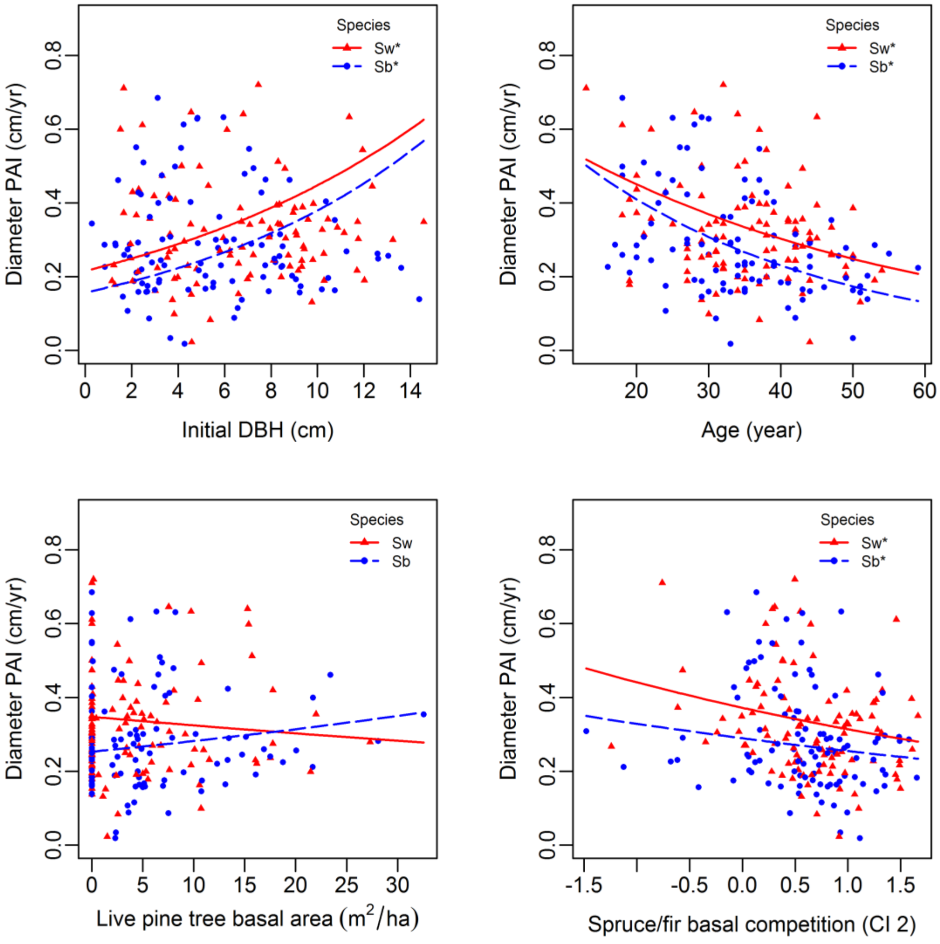

Figure 2.19 Predicted post-release diameter growth in relation to initial DBH (cm), age(years), live tree basal area (m^2/ha), and spruce/fir competition (CI 2). Lines show model estimates and symbols show values for actual data points. Average values for all variables (by species) except x-axis variable were used to calculate model estimates. All variables (including non-significant) and parameter estimates shown in Table 2.7 were included.

2.3.5 Effect of tree and stand conditions on pre and post-release height growth rate

The model developed for pre and post-release height growth rate included initial height, live tree basal area, spruce/fir competition and age. An exponential variance function (Pinheiro and Bates 2000) was used to model the variance structure in the height growth models. A plot level random effect was also incorporated in the model.

The developed height growth model is

[Eq. 2.13]

$$Y_{ijk} = (\beta_0 + b_{0i}) * \exp^{(-((\beta_1\ \text{Initial height} + \beta_2\ \text{Live tree basal area} + \beta_3 \text{Spruce/fir basal area} + \beta_4\ \text{Age})))} + \varepsilon_{ijk}$$

2.3.5.1 Pre-release height growth rate

Pre-release height growth was significantly related to initial height and age for both spruces. The relationship was positive for initial height and negative for age. Live pine tree and spruce/fir basal area did not show any significant relationship with pre-release height growth (Table 2.9 and 2.10). Residual plots of the pre-release height growth models are shown in Figure 2.20 and the plots showing fitted versus observed values (Figure 2.21) for the pre-release height growth model reveal a slight under prediction of height growth for both spruces.

2.3.5.2 Post-release height growth rate

Height growth rate following release was significantly affected by initial height, age and spruce/fir competition for both species (Table 2.10). The effect of initial height was positive for both species, i.e. taller trees increased more in height after release than shorter trees. Live pine tree basal area did not affect height growth of either species (Table 2.9 and 2.10). Post release height growth of both spruces increases with increasing spruce/fir competition and white spruce was significantly related (though marginally related in Table 2.9) to spruce/fir competition when only significant variables were included in the model (Table 2.10). The residual plot of the models revealed no obvious bias for both spruces (Figure 2.20). The fitted versus observed height growth plot are shown in Figure 2.21.

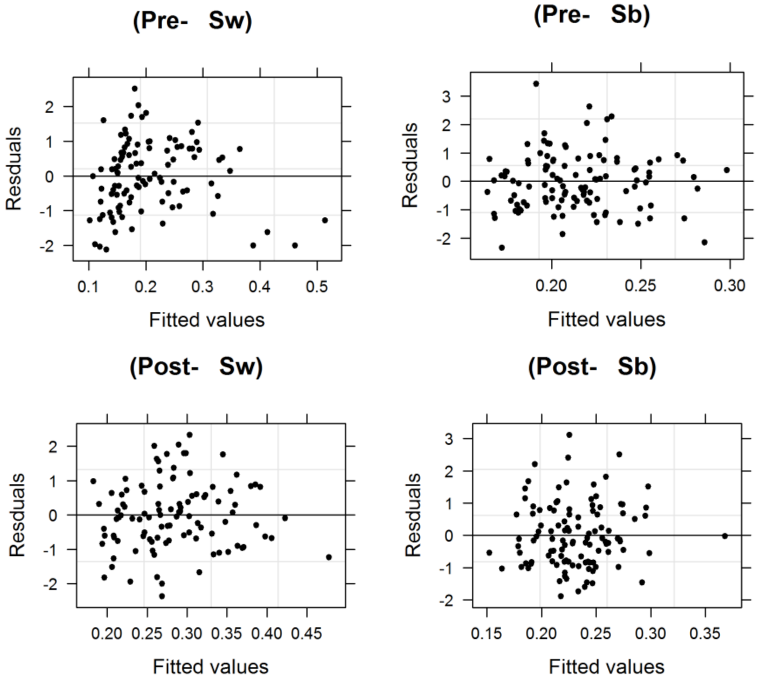

Figure 2.20 Residuals of post release height growth models for white spruce and black spruce.

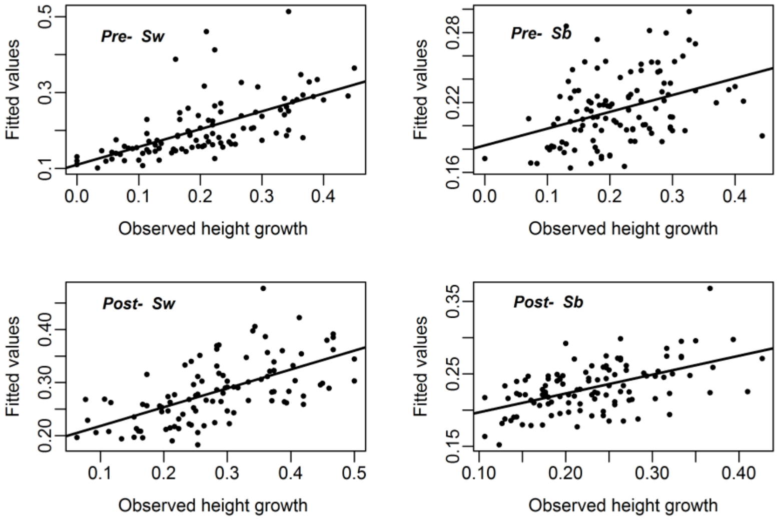

Figure 2.21 Plots of fitted versus observed pre and post-release diameter growth for white spruce and black spruce.

Table 2.9 Mixed effects models for pre-release and post release height growth rate of white and black spruce fitted with all selected variables (values in parenthesis are standard error of the estimate).

	Pre- release growth rate				**Post- release growth rate**			
Variable	**White spruce**		**Black spruce**		**White spruce**		**Black spruce**	
	Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value
Intercept	0.1246 (0.069)	**0.0004**	0.1906 (0.090)	**0.0001**	0.2514 (0.039)	**0.0010**	0.2151 (0.027)	**<0.0001**
Initial height	0.1088 (0.016)	**0.0001***	0.0651 (0.021)	**0.0016***	0.0714 (0.015)	**0.0010***	0.0472 (0.016)	**0.0038***
Live pine tree basal area	-0.0218 (0.007)	0.1022	-0.0031 (0.008)	0.5636	-0.0061 (0.005)	0.2597	0.0109 (0.004)	0.0854
Spruce/fir competition (CI2)	0.0162 (0.005)	0.8247	-0.0473 (0.069)	0.5083	0.0588 (0.063)	0.0624	0.1322 (0.060)	**0.0300***
Age	-0.0120 (0.006)	**0.0099***	-0.0064 (0.006)	**0.0011***	-0.0082 (0.006)	**0.0488***	-0.0097 (0.004)	**0.0395***

***significant at p<0.05**

Table 2.10 Simplified mixed effects models for pre-release and post release height growth rate of white and black spruce with only significant variables (values in parenthesis are standard error of the estimate).

	Pre- release growth rate				**Post- release growth rate**			
Variable	**White spruce**		**Black spruce**		**White spruce**		**Black spruce**	
	Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value
Intercept	0.1145 (0.023)	**0.0012**	0.1074 (0.048)	**0.0001**	0.2310 (0.024)	**<0.0001**	0.2040 (0.048)	**<0.0001**
Initial height	0.1293 (0.008)	**0.0008***	0.0803 (0.020)	**0.0016***	0.0726 (0.007)	**0.0010***	0.0566 (0.003)	**0.0032***
Live pine tree basal area	ns		ns		ns		ns	
Spruce/fir competition (CI2)	ns		ns		0.0713 (0.009)	**0.0431***	0.1654 (0.022)	**0.0201***
Age	-0.0157 (0.001)	**0.0052***	-0.0079 (0.005)	**0.0011***	-0.0059 (0.005)	**0.0488***	-0.0080 (0.003)	**0.0407***

***significant at $p<0.05$**

The relationship between post-release height growth rate and tree and stand variables are shown in Figure 2.22. The mean height growth rate of white spruce was higher than black spruce.

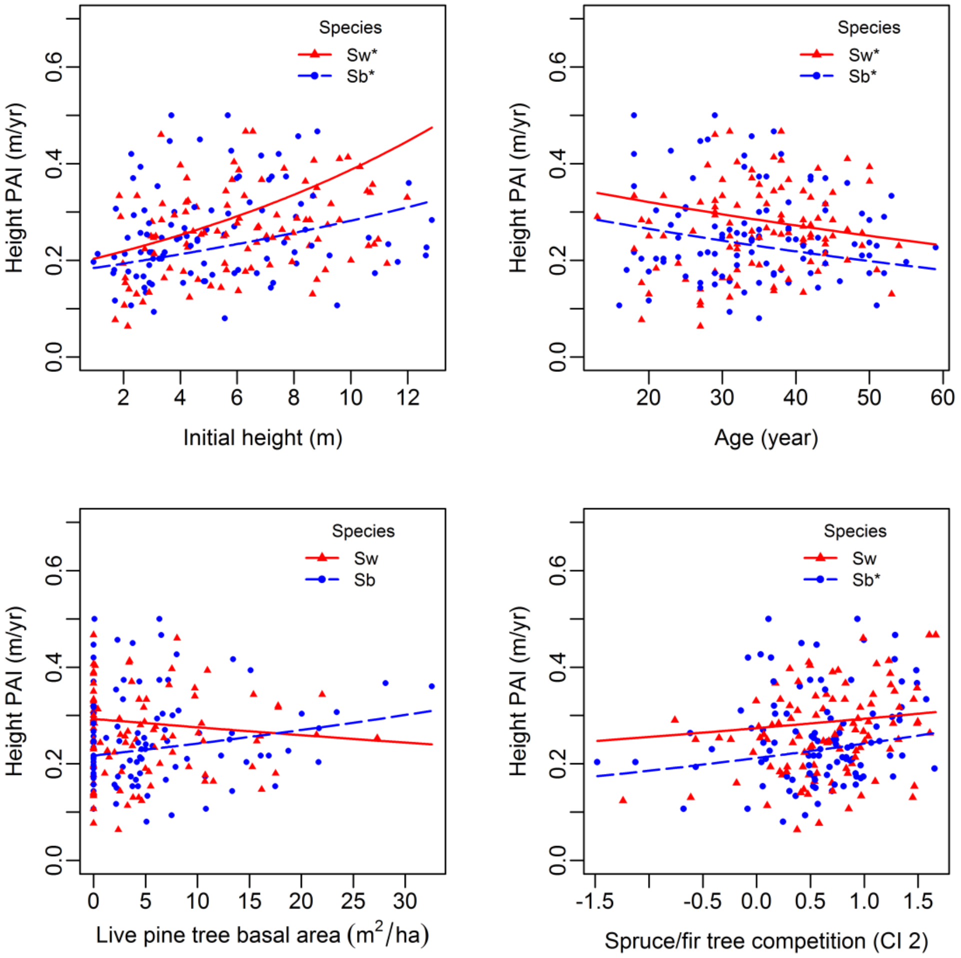

Figure 2.22 Plot showing post –release height growth rate in relation to initial height (m), age (yr), live pine tree basal area (m^2/ha) and spruce/fir competition (CI 2). Lines show model estimates and symbols show values for actual data points. Average values for all variables (by species) except the x-axis variable were used to calculate model estimates using all variables (including non-significant) and parameter estimates shown in Table 2.9.

2.3.6 Effect of tree and stand conditions on diameter and height growth ratio (release response)

The developed diameter growth ratio model was similar to the diameter growth rate model (Equation 2.12) while the height growth ratio model is similar to the height growth rate model in Equation 2.13. The plot of residuals for the diameter and height growth ratio models (Figure 2.23) and the plots of the fitted versus observed growth ratio (Figure 2.24) are presented for white and black spruce.

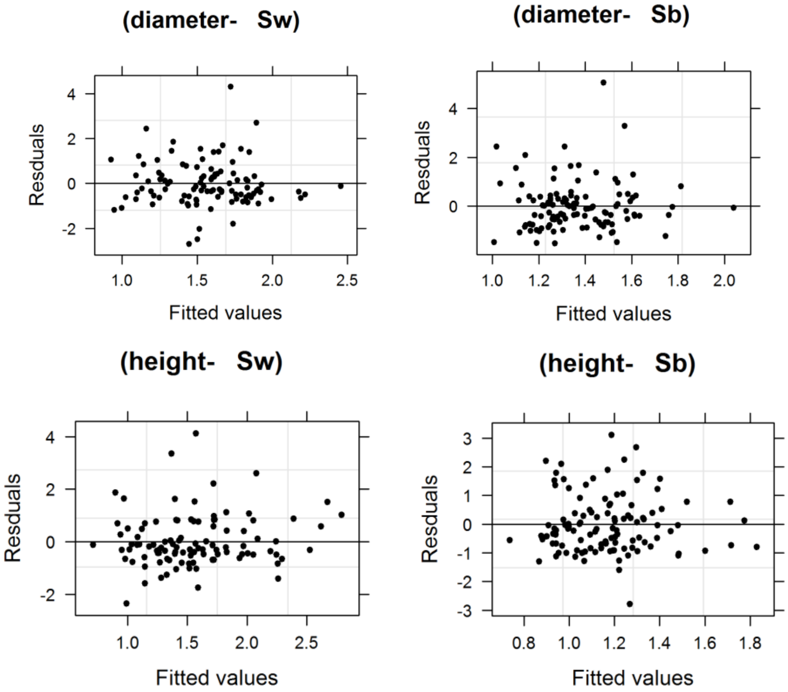

Figure 2.23 Residuals for the diameter and height growth ratio (release response) models for white spruce (Sw) and black spruce (Sb).

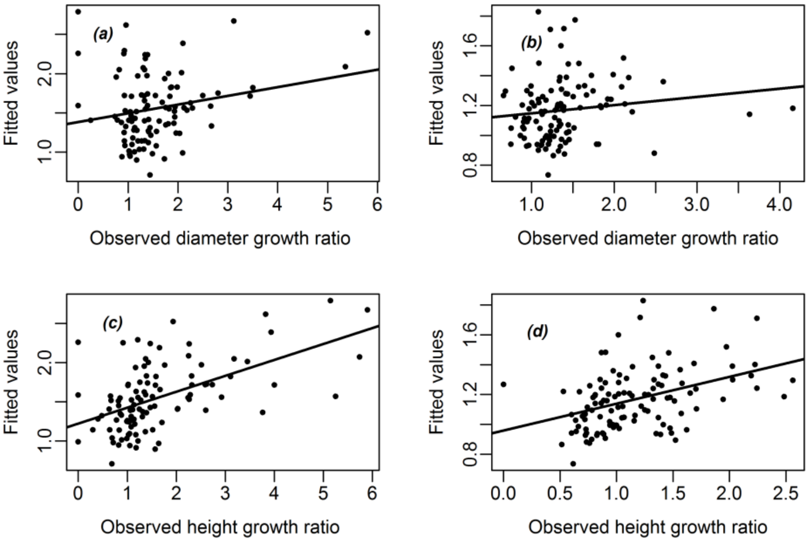

Figure 2.24 Plots of fitted versus observed post-release diameter growth ratio (release response) for white spruce (diameter (a); height (c)) and black spruce (diameter (b); height (d)).

Table 2.11 Mixed effects models for growth response ratio for white and black spruce fitted with all selected variables (values in parenthesis are standard error of the estimate).

	Diameter growth ratio				Height growth ratio			
Variable	**White spruce**		**Black spruce**		**White spruce**		**Black spruce**	
	Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value
Intercept	1.1455 (0.079)	**<0.0000**	1.0058 (0.025)	**<0.0000**	1.5204 (0.573)	**0.0001**	1.2001 (0.041)	0.3708
Initial dbh	-0.0648 (0.051)	**0.0002***	-0.0558 (0.048)	**0.0001***	-0.0143 (0.114)	0.6002	-0.0343 (0.166)	0.0925
Live pine tree basal area	-0.0047 (0.012)	0.4599	-0.0034 (0.015)	0.4155	0.0140 (0.021)	0.1733	0.0121 (0.026)	0.1288
Spruce/Fir competition (CI2)	-0.1522 (0.013)	0.0798	0.0315 (0.014)	0.6014	0.1287 (0.014)	**0.0056***	0.2716 (0.033)	**0.0002***
Age	0.0219 (0.017)	0.2040	0.0178 (0.018)	0.1007	-0.0043 (0.029)	0.6695	-0.0019 (0.034)	0.7443

***significant at p<0.05**

Table 2.12 Simplified mixed effects models for growth response ratio for white and black spruce (values in parenthesis are standard error of the estimate).

	Diameter growth ratio				**Height growth ratio**			
Variable	**White spruce**		**Black spruce**		**White spruce**		**Black spruce**	
	Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value
Intercept	1.1481 (0.112)	**<0.0000**	1.0672 (0.031)	**0.0003**	1.4866 (0.434)	**0.0004**	1.0721(0.020)	**0.0309**
Initial size (dbh or height)	-0.0553 (0.030)	**0.0005***	-0.0754 (0.016)	**0.0001***	-0.0129 (0.101)	0.3331	-0.0357 (0.064)	0.1412
Live pine tree basal area	ns		ns		ns		ns	
Spruce/Fir competition (CI2)	-0.2124 (0.098)	**0.0342***	ns		0.1503 (0.009)	**0.0042***	0.3111 (0.005)	**0.0001***
Age	ns		ns		ns		ns	

***significant at $p<0.05$**

2.3.6.1 Diameter growth ratio (release response in diameter)

Release response in diameter for white spruce and black spruce were negatively influenced by initial DBH (Tables 2.11 and 2.12). i.e smaller trees increase more in postrelease growth in relation to their pre-release growth. Live pine tree basal area and age did not significantly affect growth ratio of either spruce species. On the other hand spruce/fir competition negatively affected the diameter growth ratio of only white spruce in the simplified model (Table 2.12) though marginally significant (P<0.5) when all variables were included in the model (Table 2.11). The mean diameter growth ratio of white spruce was higher than black spruce (Figure 2.25).

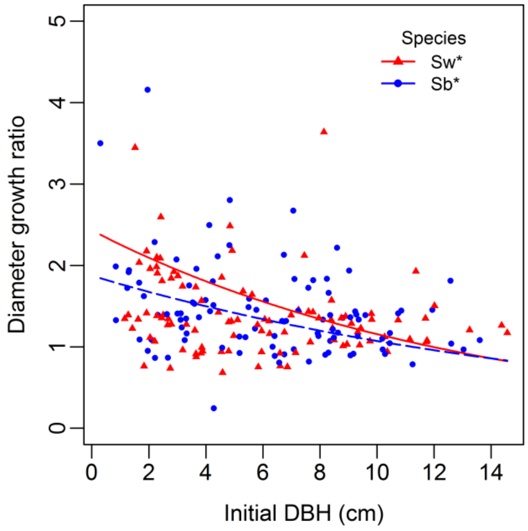

Figure 2.25 Plot showing the predicted diameter growth response against initial DBH (cm). Lines show model estimates and symbols show values for actual data points. Average values for all variables except except initial DBH were used to calculate model estimates using all variables included in Table 2.11.

2.3.6.2 Height growth response ratio (release response in height)

Release response in height for both species was only significantly affected by spruce/fir competition. The effect of spruce/fir competition was positive for both species, i.e. trees growing under higher spruce/fir competition had a higher relative height growth than trees growing under lower spruce/fir competition. On the other hand, initial height, live pine tree basal area and age did not affect height growth ratio (Table 2.11 and 2.12).

The relationship between the height growth ratio and spruce/fir basal area is shown in Figure 2.26 for both species with white spruce having a higher mean response than black spruce.

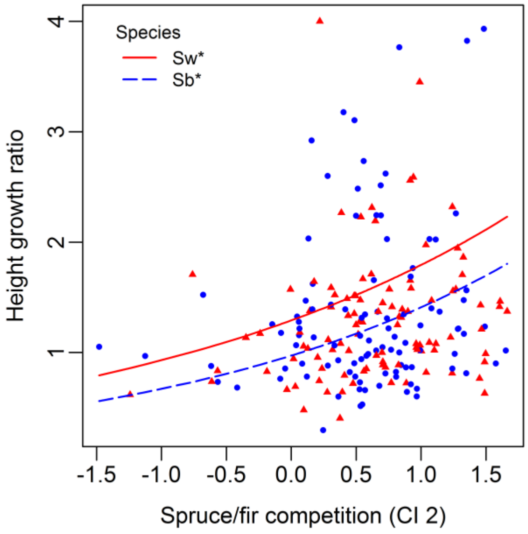

Figure 2.26 Plot showing the predicted height growth response and Spruce/fir competition (CI2). Lines describe model estimates and symbols show values for actual data points. Average values for all variables listed in Table 2.11 except spruce/fir competition were used to calculate model estimates.

2.4 Discussion

Developing management strategies for stands attacked by MPB requires an understanding of the dynamics of surviving residual trees. Affected stands that have advance regeneration have the potential to change from pine dominated stands to stands dominated by more shade tolerant species such as spruce or fir. This advance regeneration, when well spaced and in good condition, can contribute mid term harvestable volumes (Veblen et al. 1991 ; Coates et al. 2006; Pousette 2010), reducing the long-term impacts of MPB.

The growth responses of these understories has been reported to differ based on species. Some species have been found to respond better than others in MPB stands (Hawkins et al. 2013) and results from this study confirm that white spruce and black spruce respond positively to pine mortality with white spruce responding faster than black spruce. White spruce diameter growth after attack increased significantly after 4 years while black spruce increased after 6 years. Similar results were seen for height growth. White spruce height growth increased significantly after 4 years while black spruce was after 5 years. Another difference between the two spruce species is that the mean diameter increment and height growth increment after release was higher for white spruce than black spruce despite the fact that black spruce had a higher mean diameter and height than white spruce in 5 of the 7 plots sampled (Table 2.2). This might be due to the fact that black spruce grows in clusters in naturally regenerated stands (Rossi et al. 2013) and consequently experiences more competition from other understory black spruce.

Results from this study are consistent with our understanding that advance regeneration responds well after overstory mortality or thinning (Yang 1991; Stone and Wolfe 1996;

Hawkins et al. 2013; Puettmann and Saunders 2000). This study revealed that growth rates and release responses (growth ratio) were affected by initial tree size i.e larger trees and taller trees had higher post release growth rates while smaller trees had a higher growth ratio, hence, changes in the overstory canopy do not always improve conditions for understory growth (Coates and Burton 1997) since there can be variation in responses due to a wide range of individual tree sizes in naturally regenerated stands. Growth ratio was used in this study to express the release responses, i.e. changes in tree growth rates after release in relation to their pre-release growth rate. Suppressed trees with low pre-release growth rate are likely to have a higher growth ratio because due to their small size they require less biomass to show substantially changes in growth. Results from release responses (growth ratio) for diameter and height growth indicates that the smaller trees show proportionally larger response to release for both species. This result is also supported by Ruel et al. (2014). Trees with lower initial dbh are better able to maintain a balanced root to shoot ratio than larger trees (Puettmann and Saunders 2000). However, post-release growth rates and growth ratio are related (Figures 2.4 and 2.5). Post release growth rates increases with an increase in growth ratio (release response to MPB) until a threshold (2.5 for white spruce diameter and height growth ratio and ~1.8 for black spruce height growth ratio) were post-release growth starts to decrease. The decrease in post-release growth might be attributed to very small tree sizes for trees with very high release response (Figure 2.25). It will be best for forest managers to select trees with high post release growth rate (before the growth ratio threshold point) for retention since they are larger with higher volume.

Puettmann and Saunders (2000) and Ruel et al. (2014) also reported initial size as important predictors of release after overstory thinning. Initial size is important because it reflects the level of competition and suppression of a tree in a particular stand (i.e. understories that are larger or taller have relative larger available space for growth than smaller trees) as well as the size of the canopy and tree leaf area (Yang 1991; Filipescu and Comeau 2007; Diaconu et al. 2015). Results also indicates that older trees have a slower growth rate after release than younger trees. Older and smaller trees are often suppressed trees with slow pre-release growth rate. This is supported by the result of pre-release growth rate in this study. Suppressed trees with low pre-release growth are often associated with lower live crown ratio (LCR) which has been reported to be a good predictor of post-release volume growth (D'Amato et al. 2011).

Live pine tree basal area did not influence growth rates after release (except for it being marginally non-significant for post-release height and diameter growth of black spruce) which might be as a result of the sparse crowns of surviving pine following MPB outbreaks. Furthermore, only high mortality plots were used for the analysis and therefore competition effects from live pine tree were not well represented. Live pine basal area was not significant in models of pre-release growth with this probably resulting from the limited range in live pine basal area in the sampled stands prior to MPB outbreaks. Competition from spruce/fir was not related to pre-release growth (except white spruce diameter growth) since most competition in the stand before MPB outbreaks would result from overstory lodgepole pine trees (combination of live and dead pine basal area). Spruce are moderately shade tolerant trees with pre-release light levels being strongly influenced by the overstory lodgepole pine canopy. However, post-release diameter growth of both spruces was negatively affected by spruce/fir competition while post-release height growth of black spruce was positively related to spruce/fir competition. The significance of spruce/fir competition after, but not before release results from removal of the effects of the dominant pine on resources (light, water, nutrient). Furthermore, spruce/fir competition positively affected the post-release height growth of black spruce and height growth ratio of both species i.e trees growing under high spruce/fir densities have higher height growth than those growing under low densities. The fact that spruce/fir competition is associated with increases in post-release height growth reflects shifts in growth allocation and increases in height to diameter ratio associated with competition (Opio et al. 2000; Vospernik et al. 2010).

The density and structure of a stand before MPB outbreaks influences the level of suppression of trees (initial size). Low mortality plots (WC1 and WC2) had lower density than the high mortality plots and although pine mortality (release intensity) was low in these plots, spruce growth after release (Plot WC1) was better than in most of the high mortality plots. However, Plot WC2, which was a moist site, showed negative responses which may be related to increases in soil moisture (wetting up) after beetle outbreaks (BC Forest Practices Board 2007; Boon and Silins 2009). There was substantial variation in growth response of individual trees within and among plots (plot was used as a random effect for all models). This is likely a function of differences in stand and site conditions including stand structure and density, ecosite, climate, and interactions between these factors. The effect of stand density is important in these stands because it influences the amount of light available to individual trees and is also a major component of individual tree growth models used for stand projections (Knowe 1994; Nunifu 2009; Bokalo et al.

2013; Ford et al. 2017). Light levels decline as spruce/fir tree density increases in the current study. It is expected that as the advance regeneration grows their impact on light levels will increase. The effect of spruce/fir competition on light levels was likely responsible for the decreases in diameter growth response of both species.

This study explored using tree sizes (basal area per hectare), basal area distance ratio, and Heygi's competition indices measured within 5.64m and 3.99m radius as a measure of spruce/fir competition. Basal area distance ratio of spruce/fir measured at 5.64m radius was a better predictor of light than the others. Although Hegyi's competition index is a distance dependent competition index, it performs poorer than total basal area (distance independent). Inclusion of basal area of the subject tree in calculation of Hegyi's competition index is likely to have increased variability unrelated to differences in light levels since the subject tree had been removed prior to light measurement. Distance independent indices have been reported to be better than some distance dependent indices in previous studies (Filipescu and Comeau 2007; Contreras et al. 2011). Generally, competition within 5.64m radius is better related to light than using a smaller area of 3.99m. This study suggest that competition indices should not be generalized but selected for specific situations. The fact that a distance dependent competition index provides the best estimate of understory light indicates that there may be a need for forest managers to examine the spatial distribution of advance regeneration. Spatial distribution of trees within a stand can greatly determine the local environment of each individual tree as well as its development and growth (Dhar and Hawkins 2011). In addition, results suggest that, stands with a clumpy distribution of advance regeneration may require thinning to improve spruce volume growth (D'Amato et al. 2011).

Retaining advance regeneration provides a low cost opportunity for regeneration. Results show that while growth rate increases as a function of tree size at release, smaller advance regeneration respond proportionally more to release than larger trees. Management decisions to retain advance regeneration require an understanding of factors influencing responses of established tree species. Further studies are needed to provide a better understanding of the influence of factors such as wetting up on post-release growth as well as to explore the longer-term dynamics of post-MPB attacked stands.

2.5 Conclusion

Retaining advance regeneration in stands affected by MPB has a lot of ecological and economic benefits but with some degree of uncertainties. Forest managers are interested in understanding the stand dynamics and whether or not these advance growth can adequately provide mid-term timber supply. Findings from this study suggest that white and black spruce advance regeneration responded well to release (higher responses observed for white spruce) and post-release growth was positively influenced by tree size and negatively influenced by tree age and intraspecific competition. Furthermore, spruce/fir competition had a strong effect on understory light with use of a 5.64m radius plot providing better models than obtained using data from 3.99m radius plots. Although long term study of these affected stand is recommended, thinning might be required in areas with high spruce/fir densities since it has strong effects on understory light and growth rates of both spruces.

Chapter 3: Effect of climate and competition on the growth and mortality of black spruce (*Picea mariana* (Mill.) BSP.) in western boreal forests.

3.1 Introduction

Black spruce (*Picea mariana* (Mill.) BSP.) is widespread in North America and found in approximately 55% of Alaska and northern Canada's boreal forest (ACIA 2005). It is commonly found in wet sites, poor nutrient soils, and across a wide range of soil conditions including permafrost areas (Viereck et al. 1983; Iwata et al. 2012). Black spruce is of high economic value as the wood can be used for producing wood pulp and lumber. This species can grow in pure stands as well as in mixed stands with shade intolerant species like jack pine (*Pinus banksiana* Lamb), lodgepole pine (*Pinus contorta* var. latifolia Engelm.) and trembling aspen (*Populus tremuloides* Michx.) and with shade tolerant tree species including balsam fir and white spruce (Natural Resource Canada 2015).

To manage black spruce sustainably, it is important to have reliable growth and yield models. These models provide important information to forest managers to improve decision making (Cao 2014), especially in mixed stand or under the current changing climate. Having a mixed species stand of which black spruce is a component may improve resource (nutrient, water, light) utilization depending on the compatibility of tree species (Vandermeer 1989). Shade tolerant and intolerant trees can coexist due to differences in their light requirements and juvenile growth rates, for instance in mixed stands of aspen and spruce, or of pine and spruce, the shade intolerant aspen or pine has a higher juvenile growth rate and quickly occupies the site. However, the shade tolerant spruce will slowly grow up into the aspen or pine canopy and eventually dominate when aspen or pine begins to die (Peterson and Peterson 1992).

The Mixedwood Growth Model (MGM) is an individual tree–based stand growth model which was developed to help forest managers make growth and yield projections for various management options (Bokalo 2012; Bokalo et al. 2013). Importantly, growth and yield models provide a quantitative description of forest stand development and enable predictions of growth and yield needed for forest management planning (Vanclay 1994). Reliable predictions depends on developing models using reliable input data (Vanclay 2003) which implies that there is a need to improve our understanding of the relationships among factors that influence future growth and yield under different stand and site conditions and apply such understanding to modeling. Major factors influencing growth and yield include: stand composition, structure and competition (Huang et al., 2013; Cortini et al. 2012), tree size (Das 2012), climate (Battles et al. 2008; Chhin et al. 2008; Cortini et al. 2017), and site quality. Including climate variables in growth and mortality models has been shown to improve performance (Battles et al. 2008). When climate is not included in empirical models the assumption is that trees are growing under constant climatic condition which could lead to biased predictions (Pretzsch 2009; Crookston et al. 2010). Uncertainties and risks associated with forest management decisions can be reduced by integrating knowledge of climate-growth models and adaptive management (Subedi and Sharma 2013).

Diameter and height growth models are important submodels in MGM and drive stand projections. Diameter growth is a measure of tree vigor that is widely used in tree survival predictions (Yao et al. 2001) and it is closely related to photosynthetic leaf area available for tree growth and maintenance (Barnes et al. 1998). Height growth enhances the ability of a tree to compete with neighbours by exposing its leaves to more light for photosynthesis (Oliver and Larson 1996). Both diameter and height growth contribute to volume growth. Competition is often included in diameter growth and height growth models (Nunifu 2009; Huang et al. 2013). However, diameter is usually more affected by competition than height, and, as a result, height growth of dominant and co-dominant trees is widely used to estimate the site index. Another important component of growth and yield models is mortality. Most models relate the rate of tree mortality to tree size and stand characteristics (Monserud and Sterba 1999; Mailly et al. 2009; Reyes-Hernandez and Comeau 2014). Recently, Cortini et al. (2017) report that survival of black spruce is positively affected by climate moisture index, negatively affected by competition, and increases with tree size up to a threshold size. Better understanding and modelling of tree mortality is needed to improve characterization of stand dynamics and estimation of future stand conditions and yields.

Making reliable growth and yield projections depends on the compatibility among submodels including diameter and height increment and mortality models. It is important that sub models are compatible to minimize bias and several techniques have been developed with the aim of minimizing model prediction bias at the stand level (Huang and Titus 1999; Qin and Cao 2006; Nunifu 2009). Compatibility among these components is very important to achieve consistent results when forest managers attempts various alternatives in stand management (Ochi and Cao 2003). An important compatible model used in MGM is the compatible diameter growth model which is estimated using the diameter- height relationship. For example, diameter and height growth are related and a number of studies (King 1986; Wonn and O'Hara 2001) have linked this relationship to tree stability to wind and competition. Using compatible diameter growth models ensures that trees contributing to stand yield projections have forms that are ecologically realistic and consistent with stand conditions. Good predictions from compatible diameter and height increment models have been reported (Nunifu 2009). In other words open grown trees have more equitable allocation of biomass to diameter growth and height growth than trees growing in the understory of crowded stands. Growth allocation can change as trees adjust to changes in climatic conditions (Franceschini et al. 2016). For instance, increase in temperature is associated with increase in volume or height growth and a decrease in diameter growth and corresponds to a higher net carbon uptake (Way and Oren 2010). Therefore, in order to properly capture the growth allocation using compatible models, it is important to include climate variables when fitting these models. However, Ochi and Cao (2003) reported that the disadvantage of compatibility in growth and yield models is that it places constraints on the system of equations that may reduce the accuracy of the model and consequently suggested that using annual growth models provides more flexibility than compatible models which are constrained.

The use of mixed effects models (Hall and Bailey 2001) where random effects are included in the model to address the hierarchical nature of forest datasets (e.g sample plots within forest stand, trees within sample plots, and repeated measurement of trees) is known to give more reliable inferences on model parameters (Hall and Bailey 2001; Mehtätalo 2012) and enables development of parameter estimates associated with specific plots (Bailey and Clutter 1974). Mixed effects models recently developed for jack pine (Strimbu et al. 2017) for use in MGM was an improvement of the previous growth models (trembling aspen, lodgepole pine, white spruce and black spruce) which were developed without the inclusion of random effect parameter. The purpose of this study was to develop updated models of diameter growth, height growth and mortality for use in recalibrating MGM to replace black spruce functions currently used in MGM which were developed using a smaller dataset from Alberta.

Objectives

The specific objectives of this study were to:

1. Examine the effect of competition and climate on diameter and height growth;
2. Examine the effect of competition and climate on tree mortality;
3. Evaluate the effect of compatibility in fitting of the diameter growth model used in MGM.

3.2 Materials and Methods

3.2.1 Data

This study utilized permanent sample plot (PSP) data for Alberta that has been assembled in the Provincial Growth and Yield Initiative (PGYI) database which includes data for more than 5517 plots established and measured by the Government of Alberta and forest companies over the past 70 years. Available data span 8 natural subregions of Alberta (Lower Foothills, Upper Foothills, Central Mixedwood, Dry Mixedwood, Northern Mixedwood, Boreal Highlands, Montane, and Subalpine). This dataset provides a substantial increase in the number of plots available for analysis over the 699 plots that were used as the basis for survival probability functions currently implemented in MGM (Yao et al. 2001, Yang et al 2003). In addition, PSP data from Manitoba, Saskatchewan, northeastern British Columbia and Alaska were acquired for this study. Before analysis a 10% sample was randomly drawn for each forest cover type in each subregion for use in validation. Historical climate data was reconstructed using the ClimateNA computer program (Wang et al. 2012) for each PSP for the normal period 1981 to 2010.

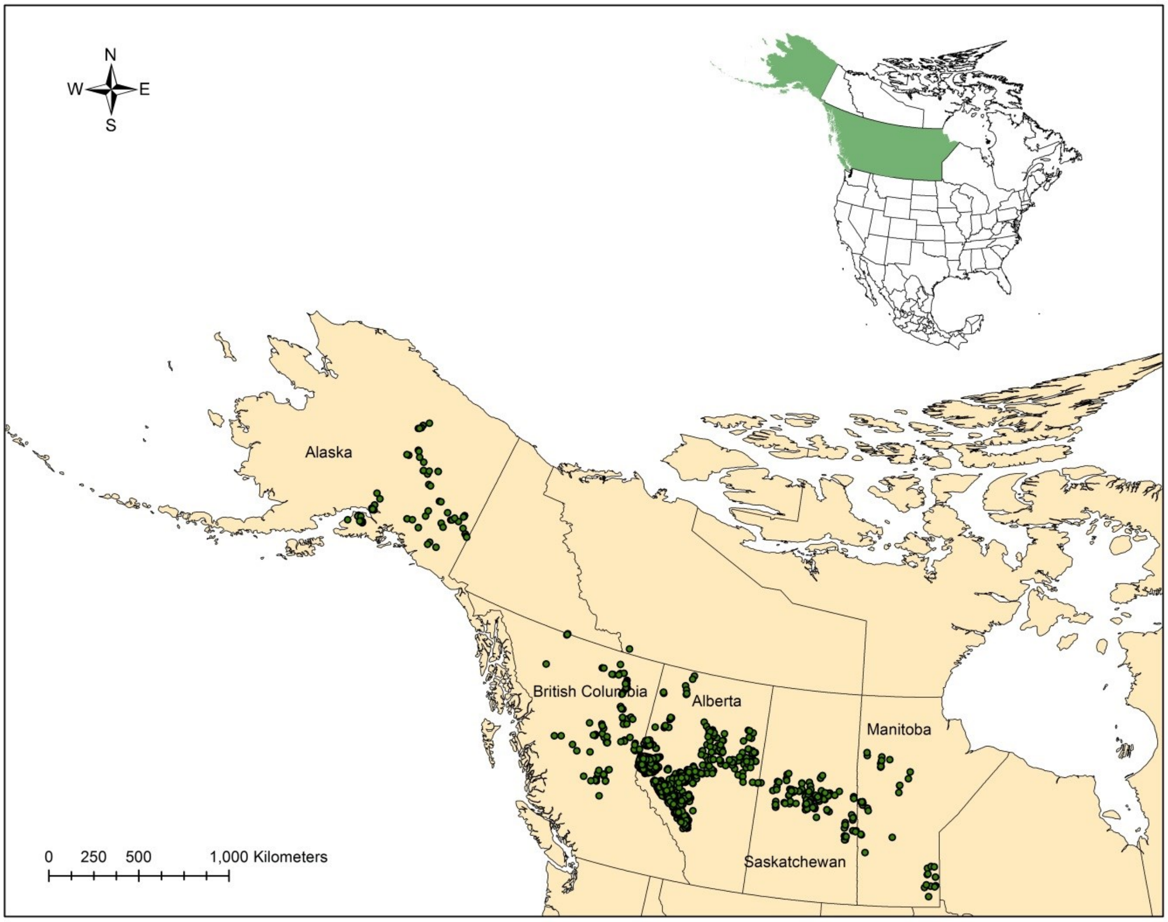

Figure 3.1. Location of plots across the different provinces and Alaska

Table 3.1. Summary statistics of tree and stand variables of black spruce trees sampled for model fitting.

Variable	Min	Mean	Max
DBH (cm)	4.01	12.71	48.70
Height (m)	2.40	11.35	34.00
Diameter Increment (cm/y)	0.003	0.121	3.000
Height Increment (m/y)	0.000	0.136	2.700
DImax (cm/y)	0.005	0.393	0.790
HImax (m/y)	0.004	0.421	0.599
Deciduous density(tph)	4.94	369.36	18400.00
Spruce/fir density (tph)	6.03	4355.04	39174.26
Pine density (tph)	4.95.	1262.65	25850.00
Deciduous BAL (m^2/ha)	0.00	3.60	30.09
Spruce/Fir BAL (m^2/ha)	0.00	16.56	119.87
Pine BAL (m^2/ha)	0.00	15.88	89.65
MAT (^{0}C)	-4.00	2.10	4.60
FFP (days)	64.00	96.94	139.00
SHM	22.50	37.21	91.50
AHM	11.70	20.48	32.60
MWMT (^{0}C)	12.00	14.54	19.00
MCMT (^{0}C)	-24.60	-10.70	-4.50
MAP (mm)	219.00	598.00	1028.00
CMI	-12.33	19.04	68.03
CMD	0.00	75.51	322.00
MSP (mm)	164.000	407.60	603.00
L (years)	1.00	11.53	45.00

DBH-diameter at breast height; DImax – maximum diameter increment; HImax – maximum height increment; BAL - basal area larger; MAT- mean annual temperature; FFP – frost free period; SHM – summer heat moisture; AHM- annual heat moisture; MWMT – mean warmest month temperature; MCMT – mean coldest month temperature; MAP- mean annual precipitation; CMI- climate moisture index; CMD- climate moisture deficit; MSP –mean summer precipitation; L – length of growth interval; tph – tree per hectare.

3.2.2 Modelling Approach and Statistical Analyses

3.2.2.1 Diameter and height model

Diameter and height increment of each tree were calculated using the formula:

$$[\text{Eq. 3.1}] \qquad Y_{\text{increment}} = \frac{Y_{t_2} - Y_{t_1}}{t_2 - t_1}$$

where: Y is DBH or Height; t_1 and t_2 are the initial and following measurement year.

There are a number of individual tree growth simulators being used today, and they can be classified according to two approaches used to predict individual tree growth within uneven-aged stands (Murphy and Shelton 1996). The first approach is called the empirical approach. This method directly fits the best relationship between measured tree growth and a selected set of predictor variables, which may or may not include a competition variable (Leak and Graber 1976, West 1980, Monserud and Sterba 1999, Zhang et al. 2004). The second approach is to predict the potential growth of a tree and then reduce that growth through a competition modifier function (Ek and Monserud 1974, Teck and Hilt 1991, Quicke et al. 1994; Lessard et al. 2001). The second approach is currently used for white spruce and aspen in MGM (Bokalo et al. 2012) and most recently jack pine (Strimbu et al. 2017) and was adopted in this study to model individual tree diameter and height growth of black spruce.

[Eq. 3.2] GROWTH = (Potential Growth) * (Modifier Function)

Potential growth was assumed to be the potential maximum diameter increment and potential maximum height increment respectively. The potential maximum diameter increment of the stand (DImax) was calculated as the average DBH increment of the thickest 100 trees/ha while the potential maximum height increment of the stand (HImax) was calculated as the average height increment of the thickest 100 trees/ha (Strimbu et al. 2017). The modifier function was expressed as a negative exponential function of a competition index for both diameter and height models. A variety of distance-independent measures of competition were selected including basal area of trees larger than the subject tree (BAL) for three competition types, namely deciduous (DecBAL), spruce/fir (SpruceFirBAL) and pine (PineBAL).

3.2.2.2 Model Specification

Mixed models were used in this study and are an improvement on previous work (Nunifu 2009; Bokalo 2012) used for the calibration of MGM. Although MGM needs only the fixed effects parameters for simulation, the nested structure of the data set violates the assumption of independence due to nesting of trees within permanent sample plots and repeated measurements of trees in the permanent sample plots (Fang and Bailey 2001). Only plot level random effects were considered for this study due to problems with non-convergence when tree level random effects were included. This was due largely to there being only a small number of repeated measurement on individual trees in the plots. The non-linear mixed model (NLME) was adopted for fitting the diameter and height growth models and follows existing procedures. The non-linear mixed model is specified as (Vonesh and Chinchilli 1997; Xu et al. 2014):

[Eq. 3.3] $$\mathrm{Y_{ijk}} = \mathrm{f}\left(\beta_{\mathrm{ij}}, \mathrm{p_{ijk}}\right) + \varepsilon_{\mathrm{ijk}},$$

$$i = 1, \dots\dots, \mathrm{a}, \mathrm{j} = 1, \dots\dots\dots, a_i, k = 1, \dots\dots, n_{ij}$$

Y_{ijk} is the k$^{\text{th}}$ response (diameter or height growth) of the j$^{\text{th}}$ tree in the i$^{\text{th}}$ plot; a is the number of plots, a_i is the number of trees within the i^{th} plot, and n_{ij} is the number of measurements per j$^{\text{th}}$ tree. f is the non linear function linking the response to the independent variables; β_{ij} is the parameter vector (g x 1); g= number of parameters in the model; p_{ijk} is the vector of the independent variables in the model (mainly competition and climate variables); ε_{ijk} is the random error which includes the within group variance and correlation (Davidian and Giltinan 1995; Xu et al. 2014).

[Eq. 3.4] $$\varepsilon_{ijk} \sim N(0, R_{ij})$$

R_{ij} is the positive definite variance-covariance structure (Davidian and Giltinan 1995).

The parameter β_{ij} can be further written as (Fang and Bailey 2001):

[Eq. 3.5] $$\beta_{ij} = A_i\beta + B_i b_i$$

$$b_i \sim N\,(0, \varphi)$$

where A_i is the r X p design matrix for the fixed effect and β is p X 1 fixed effect parameter respectively. B_i is the r X p design matrix for the random effect and b_i is the associated random effect parameter for the i$^{\text{th}}$ plot.

Parameters were considered as random or fixed effects by initially making all parameters random, and thereafter evaluating the contribution of the random effect to ascertain if some random effects could be removed (Pinheiro and Bates 2000). Since the purpose of this study is to calibrate MGM, fixed effects were selected in such a way that important competition variables (e.g. deciduous, pine and spruce basal area per hectare) which are needed for MGM simulations were significant in the final model. In other words, random effect for some parameters were eliminated in situations where they affected the inclusion of these key variables.

The variance in growth models is often found to depend on the mean and when applying the power function and exponential function, the mean response is often used as the diagonal element in the diagonal matrix of the within tree error variance (Pinheiro and Bates 2000). However, for this study, the variance function was modelled by including the independent variables as covariates and several variance functions were then compared to determine the best model. According to Pinheiro and Bates (2000), the variance functions for power and exponential models are as follows:

Power function;

[Eq. 3.6] $$g(v_{ij}, \delta) = |v_{ij}|^{\delta}$$

Exponential function;

[Eq. 3.7] $$g(v_{ij}, \delta) = \exp(\delta v_{ij})$$

where, δ is the variance parameter, v_{ij} is the variance covariate

Due to the correlation resulting from repeated measurements, an autocorrelation structure was included in the model (Pinheiro and Bates 2000). The best structure for each growth model was selected from two common correlation structures including first order autoregressive structure AR(1), continuous time autoregressive structure CAR(1) and compound symmetry (CS) (Pinheiro and Bates 2000; Fang and Bailey 2001; Xu et al. 2014). All fitting and evaluation of growth models was done in the R statistical environment (R core team 2015).

3.2.2.3 Mortality

The response variable for the mortality model was tree status, dead or alive, at the end of each growth interval. Dead tree was coded as 1 while live tree was coded as 0. Predictor variables selected were tree size and competition variables (DBH, DBH squared, deciduous, spruce/fir and pine basal area larger). Most of these selected covariates have been previously used for developing mortality or survival funtions (Yao et al. 2001; Cortini et al. 2017) and have been shown to be good predictors. For instance, trees with smaller DBH are more prone to mortality than trees of intermediate size, while very large trees may also show higher mortality rates than intermediate size trees associated with their age. While age might be a useful alternative, it is difficult to determine the ages of shade tolerant trees such as black spruce, and tree size (DBH) has been adopted as a replacement of tree age (Yao et al. 2001). The square of DBH was included to capture the U-shaped mortality trend with increasing size (Monserud and Sterba,1999; Yao et al., 2001; Reyes-Hernandez and Comeau 2014; Cortini et al. 2017) which is regarded as the ideal pattern of mortality, i.e higher mortality in smaller DBH trees followed by lower mortality as the trees get bigger and back to high mortality for very large trees (old trees). Since black spruce can grow in pure and mixed stands, competition from different types of trees (ie. intolerant deciduous, intolerant conifers, and tolerant conifers) was expected to vary and as such deciduous, spruce/fir and pine basal area larger were included as separate variables. These three competition indices are currently used in most MGM functions. In the process of model development several variables were eliminated due to multicollinearity issues.

Logistic regression is the most commonly used method for modelling individual tree mortality. Due to unequal measurement intervals, most studies have adopted the Monserud

(1976) approach, where measurement interval was used in the exponent instead of including it in the model as another predictor variable. The logit link and complementary log log link, which are both types of the binomial link functions, were tested during model development but the logit link gave better results and as such was selected. An offset variable which represents the log of time interval between two measurements was included with a coefficient set to 1 (Fortin et al., 2008; Mailly et al. 2009).

[Eq. 3.8] $$P_{ijk} = \left[\frac{\exp(\mathrm{M})}{(1+\exp(\mathrm{M}))}\right]^{L_{jk}}$$

P_{ijk} is the probability of mortality. L is the interval between successive measurements, within which tree death was observed. M was represented in the model as;

[Eq. 3.9] $$M = \beta_0 + \beta_1 x_1 + \cdots + \beta_k x_k$$

$\beta_0 \ldots\ldots \beta_k$ are parameter to be estimated. $x_1 \ldots\ldots x_k$ are the independent variables.

3.2.2.4 Incorporating climate variables into growth and mortality models

Climate variables were included in all growth and mortality functions and the effect of incorporating climate variables on model performance was evaluated. Climate averages (normals) were calculated for each plot for the period between 1981 and 2010. Climate variables tested included: mean annual temperature (MAT), mean annual precipitation (MAP), frost free period (FFP), summer heat moisture index (SHM), annual heat moisture index (AHM), climate moisture deficit (CMD) (which is the sum of the monthly difference between a reference evaporation and precipitation (Zhao et al. 2011) and it is zero when precipitation exceeds reference evaporation), mean summer precipitation (MSP) and climate moisture index (CMI) (which is an indicator of drought severity (Hogg et al.

2013)). Climate variables that were highly correlated were not included in the same model to avoid multicollinearity.

3.2.2.5 Growth model evaluation and validation

The growth models were evaluated based on goodness-of-fit criteria including log likelihood (twice the negative log-likelihood) Bayesian Information Criteria (BIC), Akaike Information Criterion (AIC) (Akaike, 1978), and visual assessment of model residuals, Lower AIC and BIC values and higher Log likelihood mean better model performance. For mortality functions, the Hosmer-Lemeshow goodness of fit test (Hosmer and Lemeshow 1989) was used to evaluate fit of the mortality models. The process involves sorting and dividing observations into 10 equal group, followed by comparison using the Pearson chi square. The inclusion of climate in the models was evaluated by comparing AIC and BIC of models without climate and models with climate. A reduction in both information criterion values indicates a significant contribution of the climate variables. Models with different climate variables were also compared with each other to ascertain their contribution as well as their relationship with growth and mortality.

Validation of all growth models without climate variables and the best model with climate was done using a validation data set (10% of reserve data). The validation metrics selected were mean error (ME), mean absolute error (MAE), root mean square error (RMSE) and relative error (RE):

[Eq. 3.10] $$\mathrm{ME} = \frac{\Sigma(y_i - \hat{y}_i)}{n}$$

[Eq. 3.11] $$\mathrm{MAE} = \frac{\Sigma\,|\mathrm{y_i} - \hat{\mathrm{y}}_\mathrm{i}|}{\mathrm{n}}$$

[Eq. 3.12] $$\mathrm{RMSE} = \sqrt{\frac{\Sigma(\mathrm{y_i} - \hat{\mathrm{y}}_\mathrm{i})^2}{\mathrm{n}}}$$

[Eq. 3.13] $$\mathrm{RE}\ (\%) = \frac{\Sigma\left[\frac{\mathrm{y_i} - \hat{\mathrm{y}}_\mathrm{i}}{\hat{\mathrm{y}}_\mathrm{i}}\right]}{\mathrm{n}}\ \mathrm{X}\ 100$$

Where n is the number of samples observed, y_i and $\hat{y}_i$ are the observed and predicted vales. Low error values from these metrics indicate a better model.

Validation of mortality without climate and the best model with climate were carried out using the same validation dataset to estimate the area under curve (AUC) which is an indicator of model performance (Sweets 1988; Cortini 2017). The better the model the more the AUC approaches one while the weaker the model the more the AUC approaches zero.

3.2.2.6 Compatible diameter-height growth model

The slope (η) which is the relationship between DBH and H is the trees ability to increase in diameter growth (Sievanem 1993). The slope η is allowed to vary with changes in tree, stand, and climatic conditions.

[Eq. 3.14] $$\frac{\partial DBH}{\partial H} = \eta$$

η is a proportionality constant (η) which is a function of competition.

The proportionality constant (η) was used as the response variable and related to stand conditions. Open grown trees are expected to have higher allocation of growth to diameter (higher η) than suppressed trees. The compatible diameter model was developed by expressing the proportionality constant as a negative exponential function of competition indices. A variety of distance-independent measures of competition were selected including basal area of trees larger than the subject tree (BAL) for three competition types, namely deciduous (DecBAL), spruce/ fir (Spruce/firBAL) and pine (PineBAL). Two sided competition measures were also examined. For example, Crowding index (CRi) which is a measure of crowding in a stand which is calculated as (TH^2Dens)/10000. TH is the species top height or dorminant height, Dens is the number of stems per hectare (Nunifu 2009).

The compatible diameter model followed the form of:

[Eq. 3.15] $$\eta = (\text{Intercept}) * \exp^{(-(\text{Tree size}+\text{Competition}+\text{Climate}))}$$

Tree size was DBH, competition includes basal area larger for deciduous, spruce/fir and pine and the climate variables were MAT, MAP and CMI.

3.2.2.7 Compatible diameter -volume growth model

The ability of a tree to allocate growth to diameter and volume can be influenced by tree factor and stand conditions. This was tested for black spruce by examining the effect of tree size, competition and climate on diameter-volume growth allocations. This relationship is presented as:

[Eq. 3.16] $$\frac{\partial DBH}{\partial Volume} = r$$

where r is the ratio between both growth and it was expressed as a function of tree size, competition and climate (similar to Equation 3.15). Volume was estimated using the honer's volume equation by incorporating the black spruce coefficients (Honer 1967) and volume increment was calculated using Equation 3.1.

Variables and model form included for this analysis were the same as used in the compatible diameter-height growth model.

3.2.2.8 Effect of including compatibility in growth model

The method currently used in MGM estimates diameter growth from height growth using a compatible diameter model (Equation 3.15). In this study, this new model will be referred to as modified compatible diameter-height growth model (MCDH).

[Eq. 3.17] $$\text{DBHincrement} = \text{htinc} * \eta$$

A modified compatible diameter-volume growth model (MCDV) was also developed using similar method;

[Eq. 3.18] $$\text{DBHincrement} = \text{volume increment} * r$$

In order to assess the effect of including compatibility in the development of a diameter growth model as currently used in MGM, MCDH (Equation 3.17) and MCDV (Equation 3.18) and the non-compatible diameter model (Equation 3.2) were compared . Comparison was done using the validation dataset and only the fixed effects estimates were used. Selected validation metrics includes ME,MAE,RMSE and RE(%) (Equations 3.10-3.13).

3.3 Results

3.3.1 Diameter growth model

The final diameter growth model (Equation 3.19 and Table 3.2) for trees larger than 4 cm dbh includes basal area larger for the three competition components (deciduous, pine and spruce/fir). A plot level random effect was included for all parameters except the parameter associated with pine basal area larger. Deciduous and coniferous competition have positive and negative effects on diameter growth of black spruce, respectively. The model was found to be significantly improved by inclusion of climate variables (Table 3.3) with CMI, CMD, SHM and MAP having a negative effect on diameter growth while MAT, FFP, AHM and MSP affected it positively. MAT had stronger influence on diameter growth than other climate variables. The predicted diameter growth (using the best model) under average conditions (averages of other variables in the model) across various ranges of DImax and climate variables are shown in Figures 3.4, 3.5 and 3.6 and Figures 3.2 and 3.3 show residual plots. DImax was included as a covariate in the variance function (i.e the error distribution increased as DImax increases). A continuous autoregressive structure (CAR(1)) was used to model the error autocorrelation. CAR1 was also appropriate because it accounts for unequal time intervals. The diameter growth models without climate (Equation 3.18) and with climate(s) (Equation 3.19 and 3.20) are :

[Eq. 3.19] Without climate:

$$\mathbf{DBH\ increment}_{\mathbf{ijk}} = \text{Max DBH increment}_{jk} * \exp^{\left(-\left((\beta_0 + b_{0i}) + (\beta_1 + b_{2i})\text{DecBAL} + (\beta_2 + b_{2i})\text{SpruceFirBAL} + \beta_3\text{PineBAL}\right)\right)} + \varepsilon_{ijk}$$

[Eq. 3.20] With one climate variable:

$$\mathbf{DBH\ increment_{ijk}} = \text{Max DBH increment}_{jk} * \exp^{(-((\beta_0 + b_{0i}) + (\beta_1 + b_{1i})\text{DecBAL} + (\beta_2 + b_{2i})\text{SpruceFirBAL} + \beta_3\text{PineBAL} + (\beta_4 + b_{4i})\text{Climate}))} + \varepsilon_{ijk}$$

[Eq. 3.21] With two climate variables:

$$\mathbf{DBH\ increment_{ijk}} = \text{Max DBH increment}_{jk} * \exp^{(-((\beta_0 + b_{0i}) + (\beta_1 + b_{1i})\text{DecBAL} + (\beta_2 + b_{2i})\text{SpruceFirBAL} + \beta_3\text{PineBAL} + (\beta_4 + b_{4i})\text{Climate}\mathbf{1} + (\beta_5 + b_{5i})\text{Climate}\mathbf{2}))} + \varepsilon_{ijk}$$

where $DBH\ increment_{ijk}$ is the increment in the ith plot, of the jth tree for the kth measurement; Max DBH increment$_{jk}$ is the maximum increment for plot ith at measurement k; $DecBAL$, $SpruceFirBAL$, and $PineBAL$ are basal area larger per hectare for deciduous, spruce and fir, and Pine; $\beta_{0,}$ $\beta_{1,}$ $\beta_{2,}$ β_3 ,$\beta_{4,}$ β_5 are the fixed effects which are to be estimated; $b_{1i,}$ $b_{2i,}$ $b_{3i,}$ b_{4i}, b_{5i} are plot level random effect.

Table 3. 2 Parameter estimates and statistical information for the diameter growth model without climate.

Fixed Effect	**Estimate**	**Std Error**	**t-value**	**Pr>|t|**	**AIC**	**BIC**
β_0 (Intercept)	0.3844	0.0075	51.0857	<0.0001	-584949.7	-584827.1
β_1 (DecBAL)	-0.0100	0.0012	-8.3842	<0.0001		
β_2 (Spruce/firBAL)	0.0243	0.0006	38.5994	<0.0001		
β_3 (PineBAL)	0.0030	0.0002	13.7792	<0.0001		
Random Effect	**Std Dev**		**VarPower (DImax)**		**Correlation CAR1**	
b_{0i} (intercept)	0.3354		0.8177		0.2951	
b_{1i} (DecBAL)	0.0250					
b_{2i} (Spruce/fir BAL)	0.0252					

Table 3.3 Parameter estimates and statistical information of fixed effects for the diameter growth model with climate parameters (standard error in parenthesis).

Eqn	**Model**	**β_0 (intercept)**	**β_1 (DecBAL)**	**β_2 (SprucefirBAL)**	**β_3 (PineBAL)**	**β_4(Climate1)**	**β_5(Climate2)**	**AIC**	**ΔAIC**
3.19	**No climate**	0.3844 (0.0075)	-0.0100 (0.0012)	0.0243 (0.0006)	0.0030 (0.0002)			-584949.7	309.3
3.20a	**MAT***	0.5354 (0.0131)	-0.0075 (0.0017)	0.0275 (0.0007)	0.0048 (0.0003)	-0.0615 (0.0053)		**-585082.3**	**176.7**
3.20b	**FFP**	0.9590 (0.0609)	-0.0062 (0.0016)	0.0278 (0.0007)	0.0045 (0.0003)	-0.0058 (0.0006)		-585021.9	237.1
3.20c	**SHM**	0.2471 (0.0246)	-0.0092 (0.0016)	0.0277 (0.0007)	0.0047 (0.0003)	0.0049 (0.0006)		-585007.2	251.8
3.20d	**AHM**	0.8341 (0.0388)	-0.0057 (0.0016)	0.0279 (0.0007)	0.0041 (0.0002)	-0.0205 (0.0019)		-585068.4	190.6
3.20e	**MAP**	0.1740 (0.0333)	-0.0063 (0.0016)	0.0281 (0.0007)	0.0041 (0.0003)	0.0004 (0.0001)		-585008.9	250.1
3.20f	**CMI**	0.3523 (0.0123)	-0.0061 (0.0016)	0.0280 (0.0007)	0.0041 (0.0003)	0.0037 (0.0004)		-585020.2	238.8
3.20g	**CMD**	0.3884 (0.0113)	-0.0086 (0.0016)	0.0278 (0.0007)	0.0046 (0.0002)	0.0005 (<0.0001)		-584974.7	284.3
3.20h	**MSP**	0.8305 (0.0380)	-0.0097 (0.0016)	0.0276 (0.0007)	0.0048 (0.0003)	-0.0010 (<0.0001)		-585064.6	194.4
3.21a	**FFP+MSP**	1.4158 (0.0724)	-0.0084 (0.0017)	0.0275 (0.0007)	0.0049 (0.0003)	-0.0061 (0.0006)	-0.0010 (0.0001)	-585145.6	113.4
3.21b	**MAT + MAP****	0.1259 (0.0340)	-0.0054 (0.0017)	0.0276 (0.0007)	0.0043 (0.0003)	-0.0933 (0.0059)	0.0008 (0.0001)	**-585259.0**	**0**

*** indicates the best model with single climate variable; ** indicates the best model with two climate variables; ns - not significant at $p<0.05$**

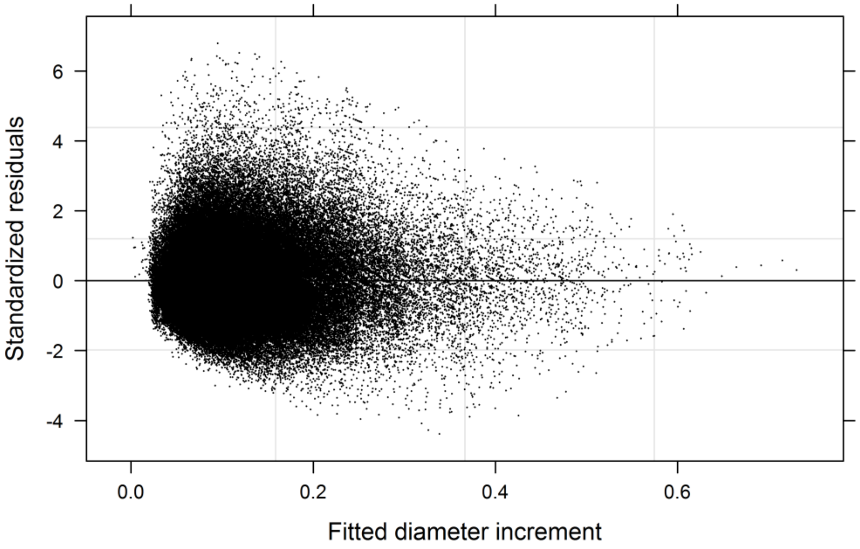

Figure 3.2 Plot of residuals for the diameter growth model without climate.

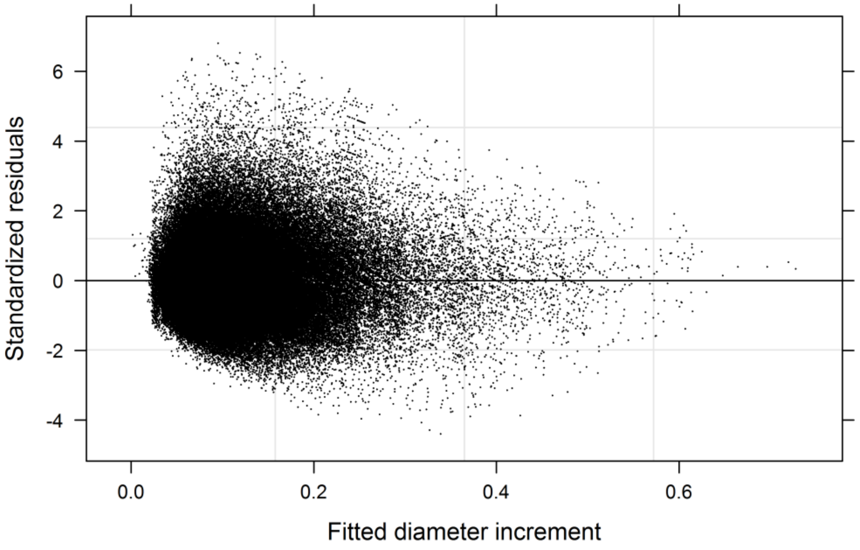

Figure 3.3 Plot of residuals for the best diameter growth model with climate.

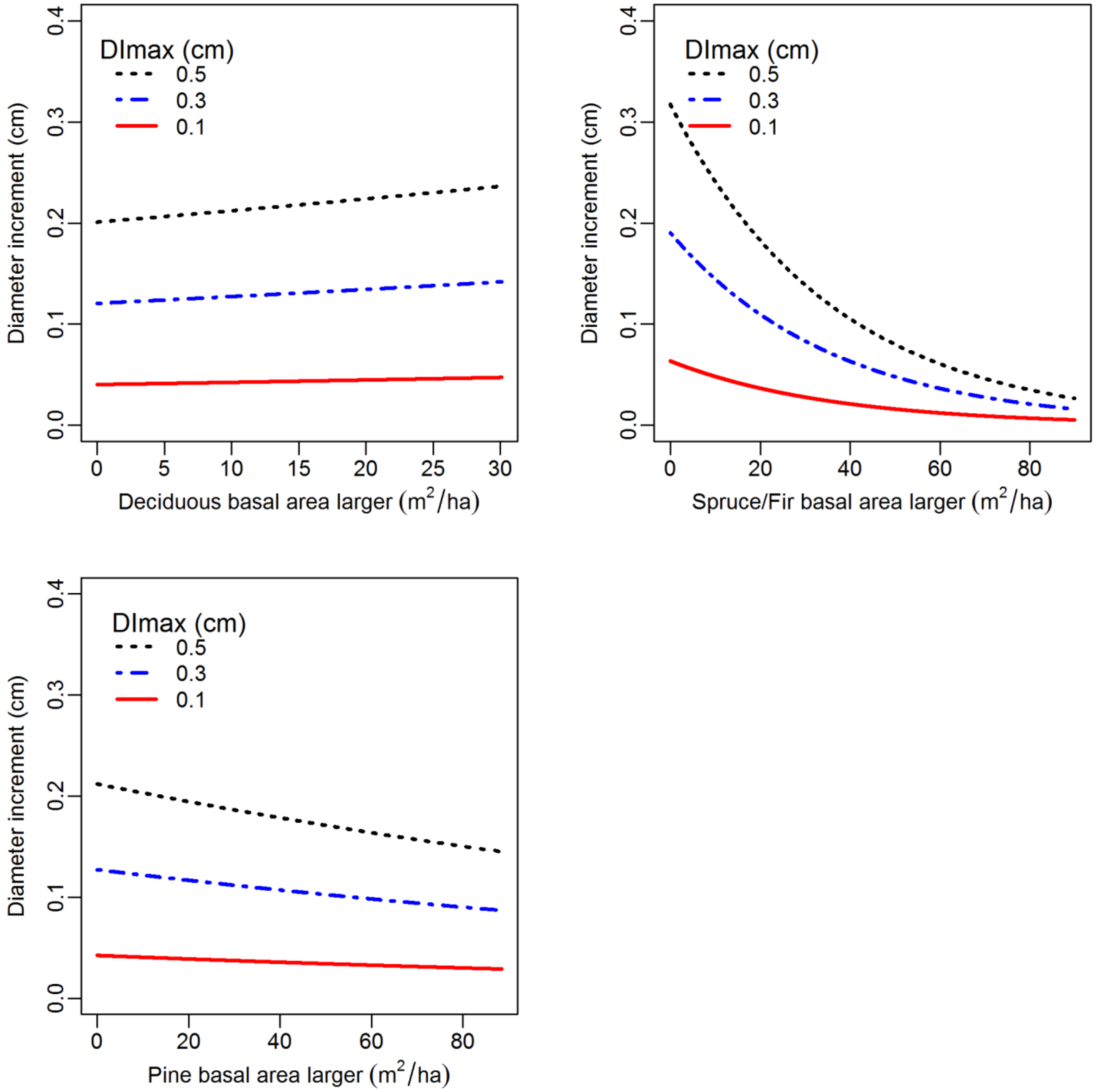

Figure 3.4 Predicted diameter increment across different conditions of maximum diameter increment (DImax) for the three competitor types - Deciduous basal area per hectare, Spruce/Fir basal area per hectare and Pine basal area per hectare.

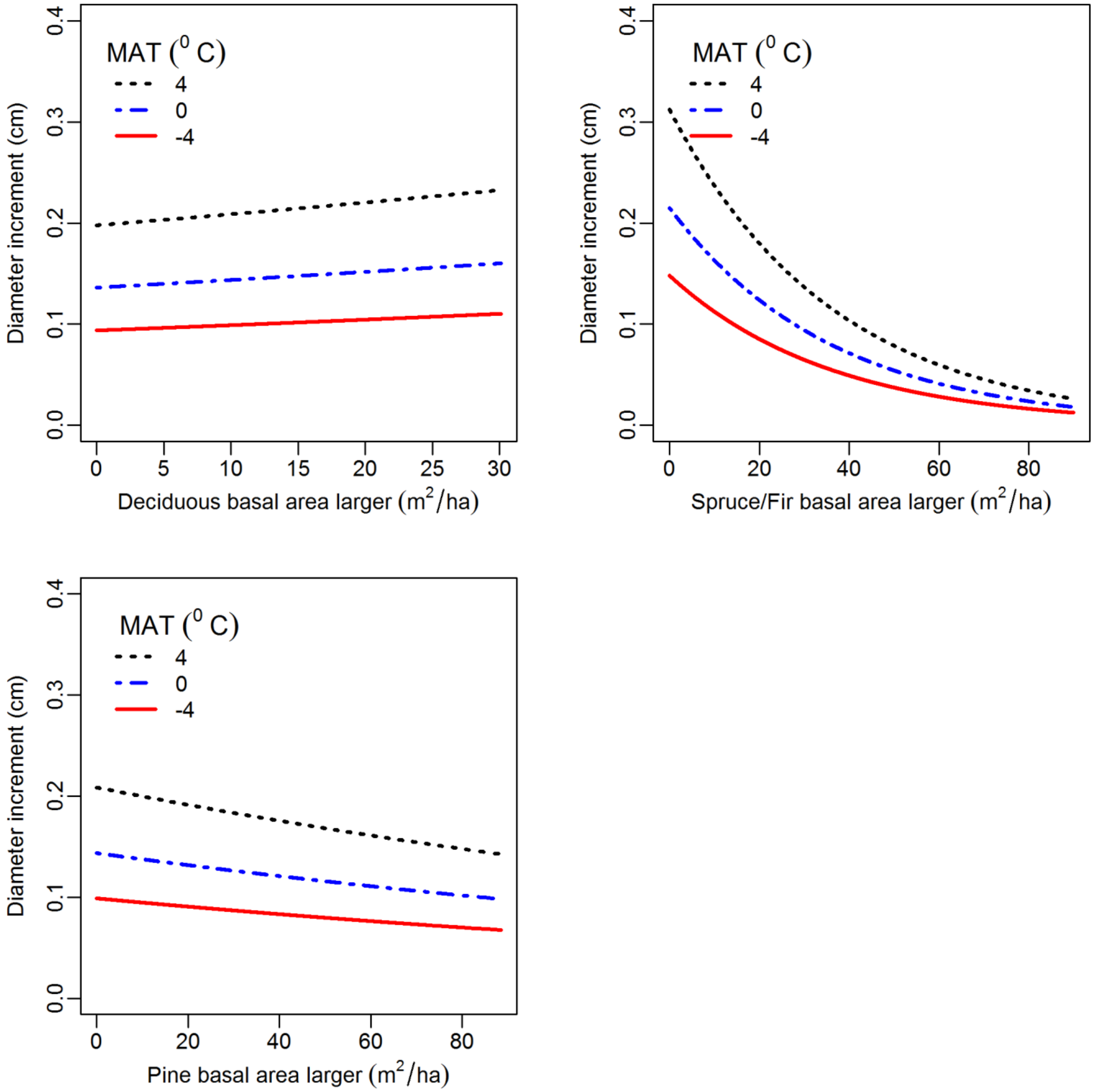

Figure 3.5 **Predicted diameter increment across different conditions of mean annual temperature (MAT) for the three competitor types - Deciduous basal area per hectare, Spruce/Fir basal area per hectare and Pine basal area per hectare.**

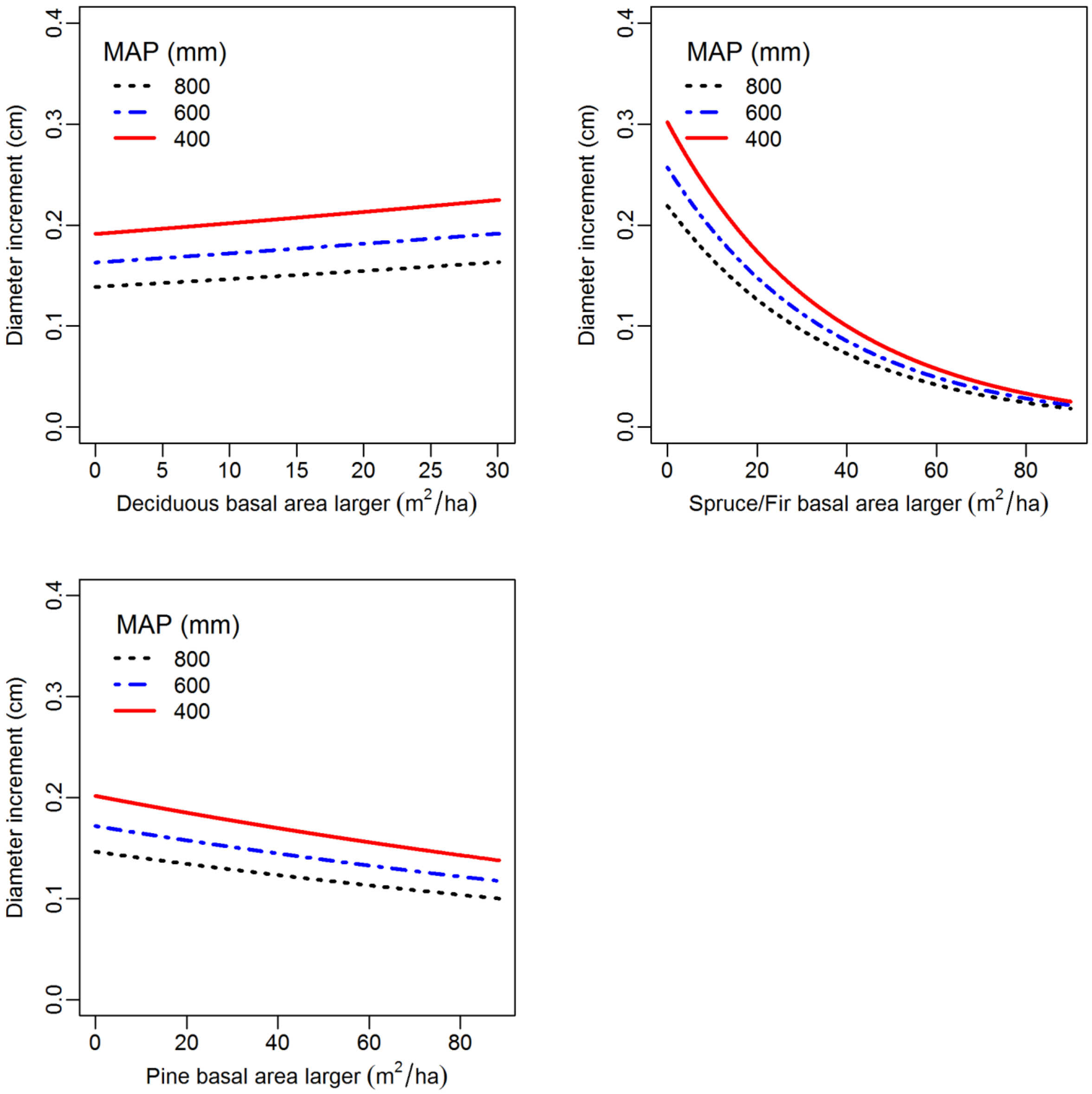

Figure 3.6 Predicted diameter increment across different conditions of mean annual precipitation (MAP) for the three competitor types- Deciduous basal area per hectare, Spruce/Fir basal area per hectare and Pine basal area per hectare.

3.3.2 Height growth model

The final height growth model (Equation 3.22 and Table 3.4) showed significant effects of basal area larger for the three competition components (deciduous, pine and spruce/fir). A plot level random effect was included for all parameters except the parameter associated with pine basal area larger (which was not significant). The effect of competition and CMI on height growth is similar to diameter growth i.e. both had negative effects. As with the diameter growth model, maximum height increment ($Max\ Height\ increment$) was included as the covariate in the variance function .i.e there was increase in the error distribution as the maximum height increment increases (Table 3.4). The CAR(1) was adopted to model dependence among observations. Including climate variables in the model was found to significantly improve the model as shown in the AIC and BIC values (Table 3.5). However, CMI and MAP were better predictors of height growth than temperature related variables such as MAT and FFP. The best model includes both MAT and MAP. Most moisture related variables positively influenced height growth while temperature related variables affected height growth negatively. The predicted height growth (using the best model) under average condition (averages of other variables in the model) across various ranges of HImax and climate variables are shown in Figures 3.9, 3.10 and 3.11.

The height growth models are as follows:

[Eq. 3.22] Without climate:

$$\boldsymbol{Height\ increment_{ijk}} = Max\ Height\ increment_{jk} * exp^{\left(-((\beta_0 + b_{0i})+(\beta_1+b_{1i})DecBAL+(\beta_2+b_{2i})SpruceFirBAL + \beta_3 PineBAL)\right)} + \varepsilon_{ijk}$$

[Eq. 3.23] With one climate variable:

$$\boldsymbol{Height\ increment_{ijk}} =$$

$$Max\ Height\ increment_{jk} *$$

$$exp^{\left(-((\beta_0+ b_{0i})+(\beta_1+b_{1i})DecBAL+(\beta_2+b_{2i})SpruceFirBAL\ +\ \beta_3 PineBAL+(\beta_4+b_{4i})Climate)\right)} + \varepsilon_{ijk}$$

[Eq. 3.24] With two climate variables:

$$Max\ Height\ increment_{jk} *$$

$$exp^{\left(-((\beta_0+ b_{0i})+(\beta_1+b_{1i})DecBAL+(\beta_2+b_{2i})SpruceFirBAL\ +\ \beta_3 PineBAL+(\beta_4+b_{4i})Climate\mathbf{1}+(\beta_5+b_{5i})Climate\mathbf{2}\ )\right)} +$$

$$\varepsilon_{ijk}$$

Where $Height\ increment_{ijk}$ is the increment in the ith plot, of the jth tree for the kth measurement; Max Height increment$_{jk}$ is the maximum increment for plot ith at measurement k; $DecBAL,\ SpruceFirBAL,\ and\ PineBAL$ are basal area larger per hectare for deciduous, spruce and fir, and Pine; $\beta_{0,}$ $\beta_{1,}$ $\beta_{2,}$ $\beta_{3\ ,}$ $\beta_{4,}$ β_5 are the fixed effects which are to be estimated; $b_{1i,}$ $b_{2i,}$ $b_{3i\ ,}$ $b_{4i,}$ b_{5i} are plot level random effect .

Table 3.4. Parameter estimates and statistical information for the height growth model without climate.

Fixed Effect	**Estimate**	**Std Error**	**t-value**	**Pr>|t|**	**AIC**	**BIC**
β_0 (Intercept)	0.6935	0.0094	73.620	<0.0001	-473018.4	-472895.9
β_1 (DecBAL)	-0.0151	0.0014	-10.6238	<0.0001		
β_2 (Spruce/fir BAL)	0.0140	0.0005	25.5892	<0.0001		
β_3 (Pine BAL)	0.0018	0.0003	6.7034	<0.0001		
Random Effect	**Std Dev**		**VarExp (HImax)**		**Correlation CAR1**	
b_{0i} (intercept)	0.42833		2.0434		0.1309	
b_{1i} (DecBAL)	0.03192					
b_{2i} (Spruce/fir BAL)	0.01902					

Table 3.5. Parameter estimates, AIC and ΔAIC for height growth models with climate showing only fixed effect parameters (standard error in parenthesis).

Eqn	Model	β_0 (intercept)	β_1 (DecBAL)	β_2 (SpruceFirBAL)	β_3 (PineBAL)	β_4 *(Climate)*	β_5 *(Climate)*	AIC	ΔAIC
3.22	**No climate**	0.6935	-0.0151	0.0140	0.0018				
		(0.0094)	(0.0014)	(0.0005)	(0.0003)				
3.23a	**MAT**	0.7123	-0.0152	0.0140	0.0019	-0.0076		-473018.7	131.1
		(0.0135)	(0.0014)	(0.0005)	(0.0003)	(0.0054)			
3.23b	**FFP**	0.9794	-0.0146	0.0140	0.0018	-0.0030		-473037.6	112.2
		(0.0613)	(0.0014)	(0.0006)	(0.0003)	(0.0006)			
3.23c	**SHM**	0.7082	-0.0150	0.0140	0.0017	-0.0004		-473017.3	132.5
		(0.0255)	(0.0014)	(0.0006)	(0.0003)	(0.0006)			
3.23d	**AHM**	1.0659	-0.0137	0.0141	0.0014	-0.0185		-473114.4	35.4
		(0.0392)	(0.0014)	(0.0006)	(0.0003)	(0.0019)			
3.23e	**MAP**	0.3818	-0.0139	0.0143	0.0013	0.0005		-473115.3	34.5
		(0.0332)	(0.0014)	(0.0006)	(0.0003)	(0.0001)			
3.23f	**CMI***	0.6099	-0.0137	0.0141	0.0013	0.0045		**-473124.5**	**25.3**
		(0.012)	(0.0014)	(0.0006)	(0.0003)	(0.0004)			
3.23g	**CMD**	0.7170	-0.0145	0.0141	0.0016	-0.0003		-473028.2	121.6
		(0.0118)	(0.0014)	(0.0005)	(0.0003)	(0.0001)			
3.23h	**MSP**	0.7796	-0.0157	0.0140	0.0019	-0.0002		-473020.9	128.9
		(0.0389)	(0.0015)	(0.0006)	(0.0002)	(0.0001)			
3.24a	**FFP+CMI**	0.8982	-0.0131	0.0141	0.0013	-0.0031	0.0045	-473143.1	6.7
		(0.0625)	(0.0014)	(0.0006)	(0.0003)	(0.0007)	(0.0004)		
3.24b	**MAT + MAP****	0.3589	-0.0137	0.0141	0.0014	-0.0359	0.0007	**-473149.8**	**0**
		(0.0337)	(0.0014)	(0.0005)	(0.0002)	(0.0060)	(0.0001)		

*** indicates the best model with single climate variable; ** indicates the best model with two climate variables; ns - not significant at $p<0.05$**

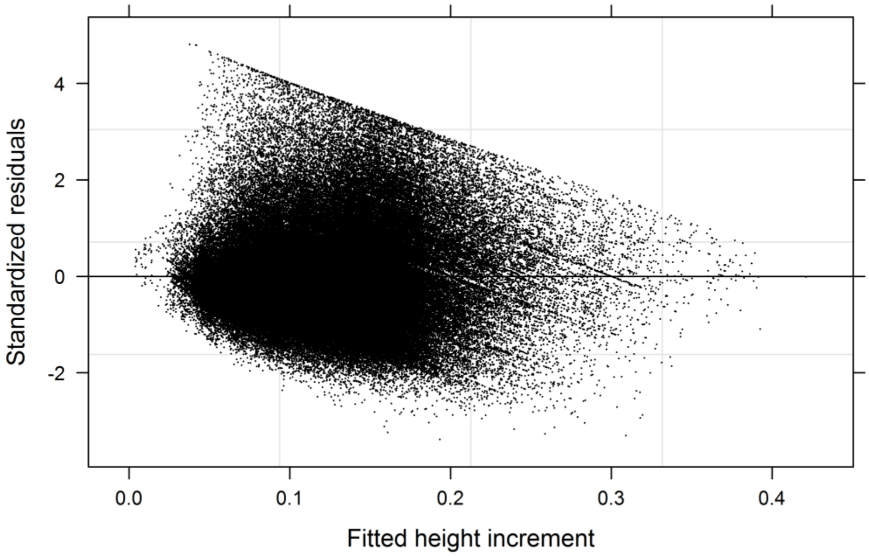

Figure 3.7 Plot of residuals for the height growth model without climate.

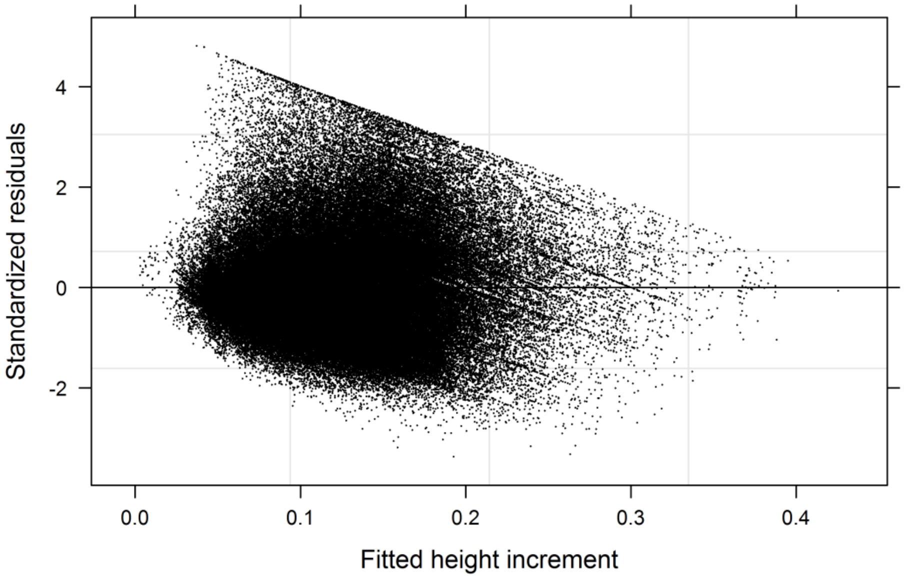

Figure 3.8 Plot of residuals for the best height growth model with climate.

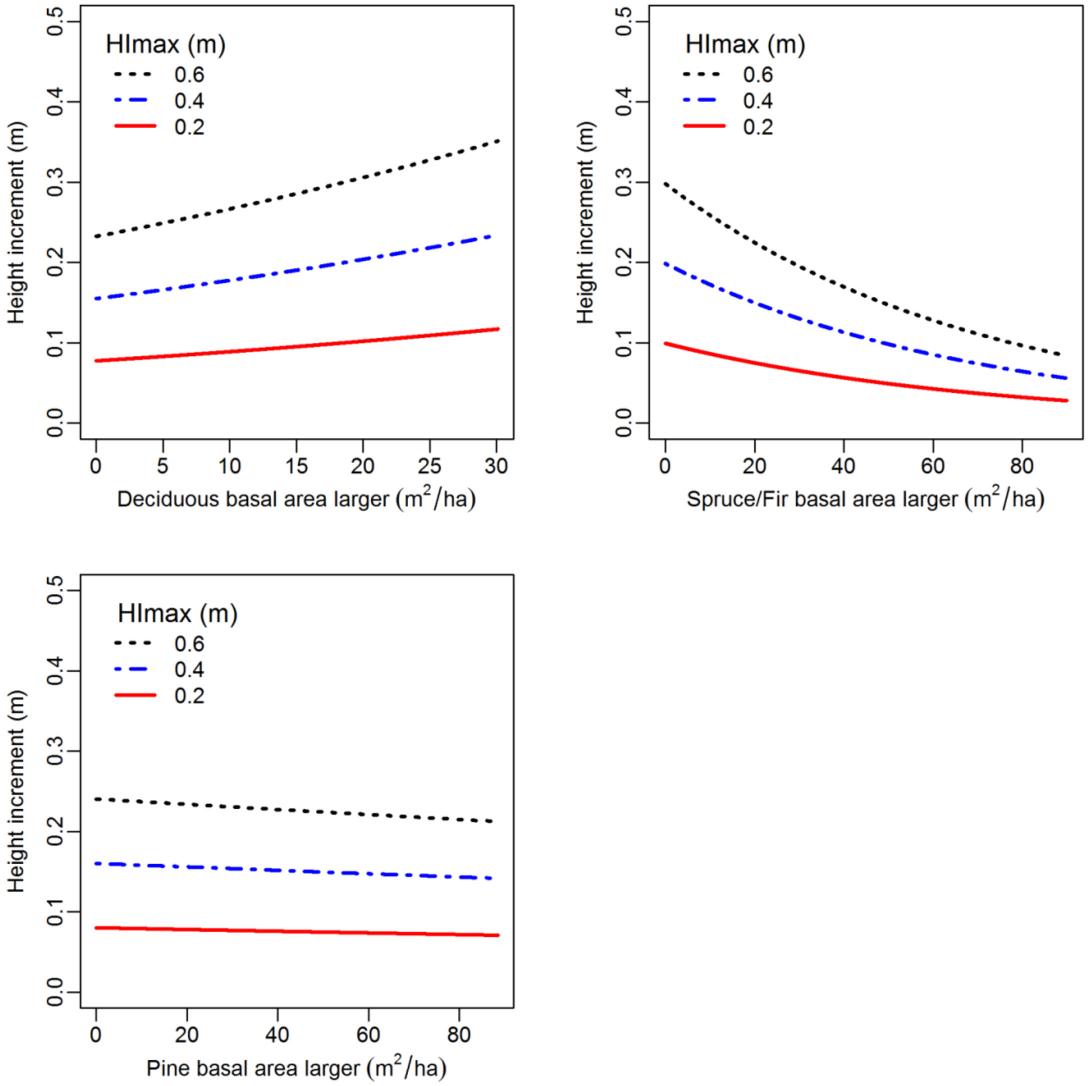

Figure 3.9 **Predicted height increment across different conditions of maximum height increment (HImax) for the three competitor types- Deciduous basal area per hectare, Spruce/Fir basal area per hectare and Pine basal area per hectare.**

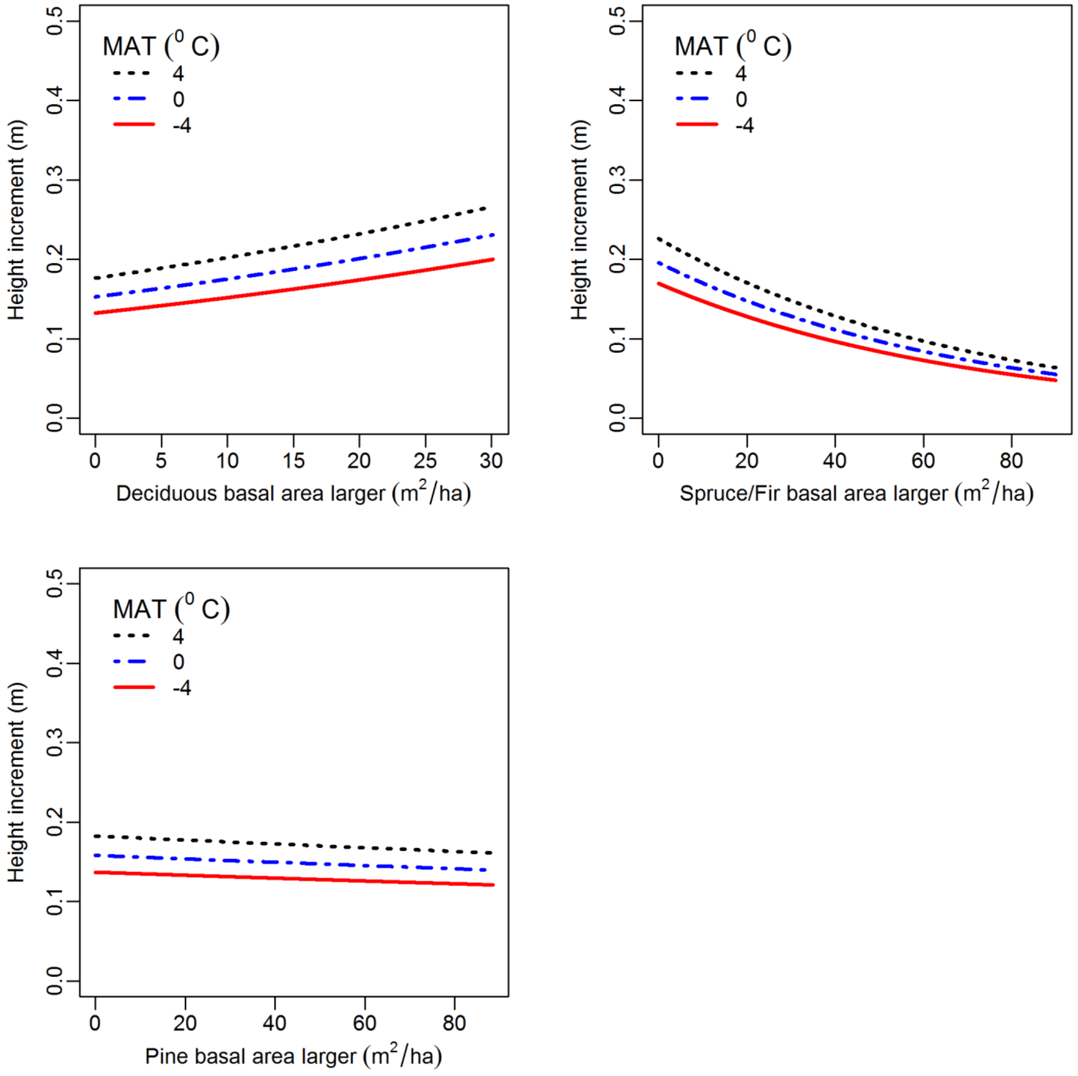

Figure 3.10 Predicted height increment across different conditions of mean annual temperature (MAT) for the three competitor types- Deciduous basal area per hectare, Spruce/Fir basal area per hectare and Pine basal area per hectare.

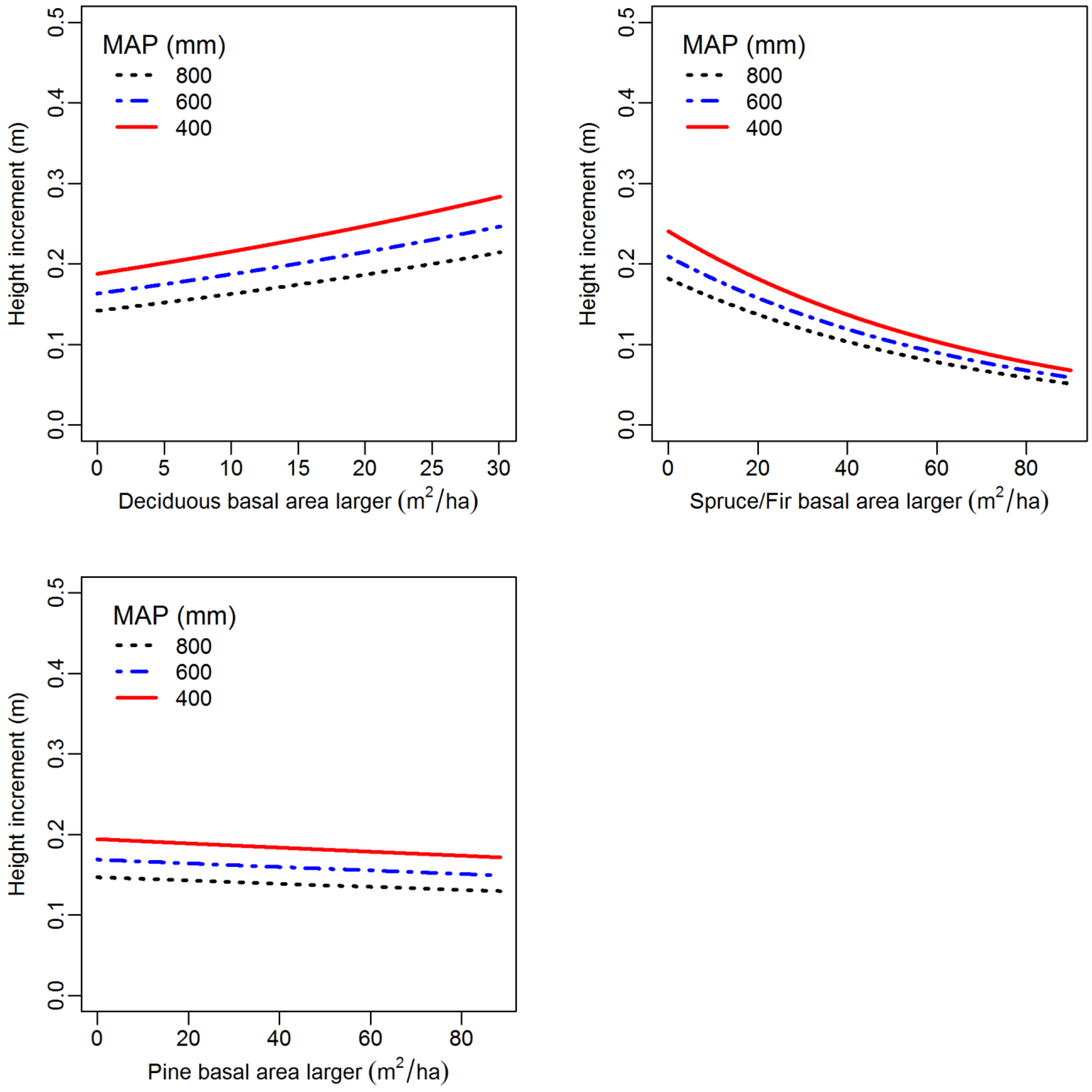

Figure 3.11 Predicted height increment across different conditions of mean annual precipitation (MAP) for the three competitor types- Deciduous basal area per hectare, Spruce/Fir basal area per hectare and Pine basal area per hectare.

3.3.3 Validation of diameter and height growth models

The validation dataset is summarized in Table 3.6. It shows the variables included in all growth functions including their means, minimum and maximum values. Using the validation dataset, comparison between fitted values and observed values as reported by various validation metrics show that the error rate across models is minimal which is indicative of satisfactory fits. All error values across all validation metrics are lower for Model including climate variables (Table 3.7).

Table 3.6. Summary of the validation dataset .

Variable	Min	Mean	Max
DBH (cm)	3.85	12.45	40.80
Height (m)	2.74	11.41	29.10
Diameter Increment (cm)	0.004	0.113	1.188
Height Increment (m)	0.002	0.130	0.596
DImax (cm)	0.007	0.211	1.188
HImax (cm)	0.004	0.268	0.597
Deciduous BAL (m^2/ha)	0.00	3.38	28.01
SpruceFir BAL (m^2/ha)	0.00	16.65	110.56
Pine BAL (m^2/ha)	0.00	11.41	70.37
MAT (^{0}C)	-6.50	1.99	4.50
FFP (days)	67.00	96.00	109.00
MAP (mm)	213.00	595.20	871.00
CMI	-14.46	18.63	50.33
CMD	50.33	73.79	279.00
MSP (mm)	160.0	410.9	567.0
L (years)	1.00	11.28	32.00

DBH-diameter at breast height; DImax – maximum diameter increment; HImax – maximum height increment; BAL - basal area larger; MAT- mean annual temperature; FFP – frost free period; MAP- mean annual precipitation; CMI- climate moisture index; CMD- climate moisture deficit; MSP –mean summer precipitation; L – length of growth interval.

Table 3.7. Validation of growth functions (ME=Mean error ; MAE= Mean absolute error; RMSE= Root mean square error; RE= Relative error).

	ME	MAE	RMSE	RE (%)
Diameter	0.0222	0.0493	0.0674	39.19
Diameter with climate	0.0186	0.0487	0.0666	31.54
Height	0.0232	0.0628	0.0830	32.16
Height with climate	0.0221	0.0628	0.0828	32.10

3.3.4 Mortality functions for black spruce

DBH, DBH^2 and Basal area larger of deciduous, spruce/fir and pine were important predictors of mortality. Tree size (DBH) was negatively related to mortality and DBH squared was positively related to mortality (i.e. mortality decreases as trees increase in size with mortality increasing as tree size becomes very large due to the effect of DBH^2). As expected, competition from larger trees (BALarger) increases mortality (Table 3.8). All climate variables improved model performance (Higher AIC and AUC values) except CMI and AHM. Results also revealed that SHM was negatively related to mortality while MAT, FFP, CMD, MAP and MSP were positively related to mortality. MSP had the strongest influence on mortality (Table 3.8). The predicted probability of mortality using selected models under average conditions (averages of other variables in the model) across various ranges of DBH, competition types and climate variables are shown in Figures 3.12, and 3.13.

The Hosmer-Lemeshow goodness-of-fit test shows the observed and expected dead trees as well as the difference between them (Table 3.9) for mortality function without climate (Equation 3.25). The difference was not significantly different at $\alpha = 0.05$.

The fitted mortality function with and without climate variables are:

[Eq. 3.25] Without climate:

$$\mathbf{M1}: \mathrm{Pm} = \beta_0 + \beta_1\mathrm{DBH}_{ijk} + \beta_2\mathrm{DBH}_{ijk}^2 + \beta_3\mathrm{Dec\ BAL}_{jk} + \beta_4\mathrm{SpruceFir\ BAL}_{jk} + \beta_5\mathrm{Pine\ BAL}_{jk}$$

[Eq. 3.26] With one climate variable:

$$\mathbf{M2}: \mathrm{Pm} = \beta_0 + \beta_1\mathrm{DBH}_{ijk} + \beta_2\mathrm{DBH}_{ijk}^2 + \beta_3\mathrm{Dec\ BAL}_{jk} + \beta_4\mathrm{SpruceFir\ BAL}_{jk} + \beta_5\mathrm{Pine\ BAL}_{jk} + \beta_6\mathrm{Climate}_{ij}$$

[Eq. 3.27] With two climate variables:

$$\mathbf{M3}: \mathrm{Pm} = \beta_0 + \beta_1\mathrm{DBH}_{ijk} + \beta_2\mathrm{DBH}_{ijk}^2 + \beta_3\mathrm{Dec\ BAL}_{jk} + \beta_4\mathrm{SpruceFir\ BAL}_{jk} + \beta_5\mathrm{Pine\ BAL}_{jk} + \beta_6\mathrm{Climate1}_{ij} + \beta_7\mathrm{Climate2}_{ij}$$

Table 3.8. Parameter estimates and AIC values for mortality functions with and without climate (standard error in parenthesis).

Eqn	**Model**	**β_0 (intercept)**	**β_1 (DBH)**	**β_2 (DBH^2)**	**β_3 (Deciduous)**	**β_4 (Spruce/fir)**	**β_5 (Pine)**	**β_6(Climate)**	**β_7(Climate)**	**AIC**	**ΔAIC**
3.25	**No climate**	-2.3096	-0.1705	0.0058	0.0050	0.0024	0.0047			19957	448
		(0.1058)	(0.0132)	(0.0004)	(0.0021)	(0.0013)	(0.0012)				
3.26a	**MAT**	-3.3770	-0.1774	0.0057	0.0103	0.0074	0.0175	0.3254		19772	263
		(0.1305)	(0.0136)	(0.0004)	(0.0021)	(0.0012)	(0.0010)	(0.0267)			
3.26b	**FFP**	-4.9450	-0.1418	0.0049	0.0099	0.0070	0.0226	0.0240		19824	315
		(0.2561)	(0.0134)	(0.0004)	(0.0021)	(0.0013)	(0.0010)	(0.0021)			
3.26c	**SHM**	-0.8084	-0.2036	0.0064	0.0115	0.0067	0.0152	-0.0311		19821	312
		(0.1648)	(0.0137)	(0.0004)	(0.0021)	(0.0013)	(0.0011)	(0.0290)			
3.26d	**AHM**	-1.9593	-0.1741	0.0058	0.0100	0.0063	0.0191	-0.0153 **ns**		19956	447
		(0.2594)	(0.0135)	(0.0004)	(0.0021)	(0.0013)	(0.0010)	(0.0093)			
3.26e	**MAP**	-3.4165	-0.1840	0.0060	0.0101	0.0083	0.0175	0.0021		19902	393
		(0.1985)	(0.0136)	(0.0004)	(0.0021)	(0.0013)	(0.0010)	(0.0003)			
3.26f	**CMI**	-2.2761	-0.1697	0.0057	0.0115	0.0083	0.0197	-0.0023		19958	449
		(0.1183)	(0.0135)	(0.0004)	(0.0022)	(0.0013)	(0.0010)	(0.0022)			
3.26g	**CMD**	-1.7456	-0.1924	0.0061	0.0102	0.0061	0.0164	0.0043		19863	354
		(0.1210)	(0.0136)	(0.0004)	(0.0020)	(0.0013)	(0.0010)	(0.0452)			
3.26h	**MSP***	-4.1932	-0.2113	0.0065	0.0107	0.0071	0.0135	0.0057		**19720**	**211**
		(0.1901)	(0.0137)	(0.0004)	(0.0023)	(0.0013)	(0.0011)	(0.0004)			
3.27	**FFP+MSP**	-7.9983	-0.1884	0.0059	0.0111	0.0084	0.0156	0.0319	0.0067	**19509**	**0**
	******	(0.3226)	(0.0136)	(0.0004)	(0.0019)	(0.0013)	(0.0011)	(0.0022)	(0.0004)		

*** indicates the best model with single climate variable; ** indicates the best model with double climate variables; ns – not significant**

Table 3.9. Hosmer-Lemeshow goodness of fit test for model 3.24 (without climate).

Group	**Total no. of trees**	**No. of dead trees**		
		Observed	**Expected**	**Difference**
1	5149	123	165	-42
2	5148	172	182	-10
3	5148	162	195	-33
4	5148	192	207	-15
5	5148	222	220	2
6	5148	248	235	13
7	5148	288	254	34
8	5148	307	282	25
9	5148	356	331	25
10	5149	508	505	3
Total	51482	2578	2576	2

Hosmer-Lemeshow satstistics=28.4 with 8 df (p=0.052)

The area under curve for the Equation 3.24 (without climate) and Equation 3.26a (with climate –best) indicates that both models are satisfactory. However, the model including two climate variables (FFP and MSP) shows a better fit (AUC=0.616) than the model without climate (AUC=0.555).

Table 3.10. Mortality model validation for functions with and without climate.

Model	**AUC**
Equation 26 (without climate)	0.555
Equation 28 (with climate –best)	0.616

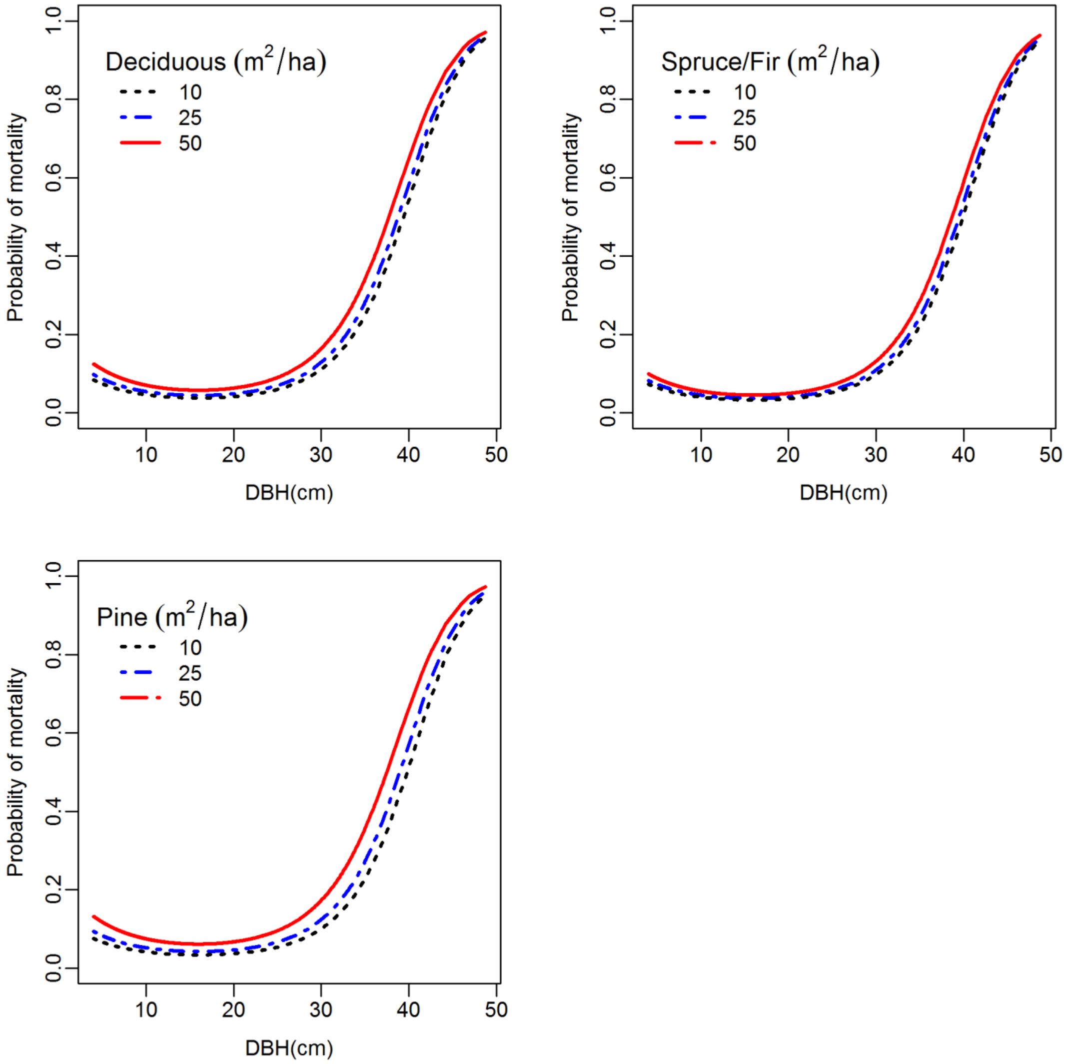

Figure 3.12. Predicted mortality across DBH under different competition types (m^2/ha) - (a) Deciduous basal area larger; (b) Spruce/fir basal area larger, and (c) Pine basal area larger.

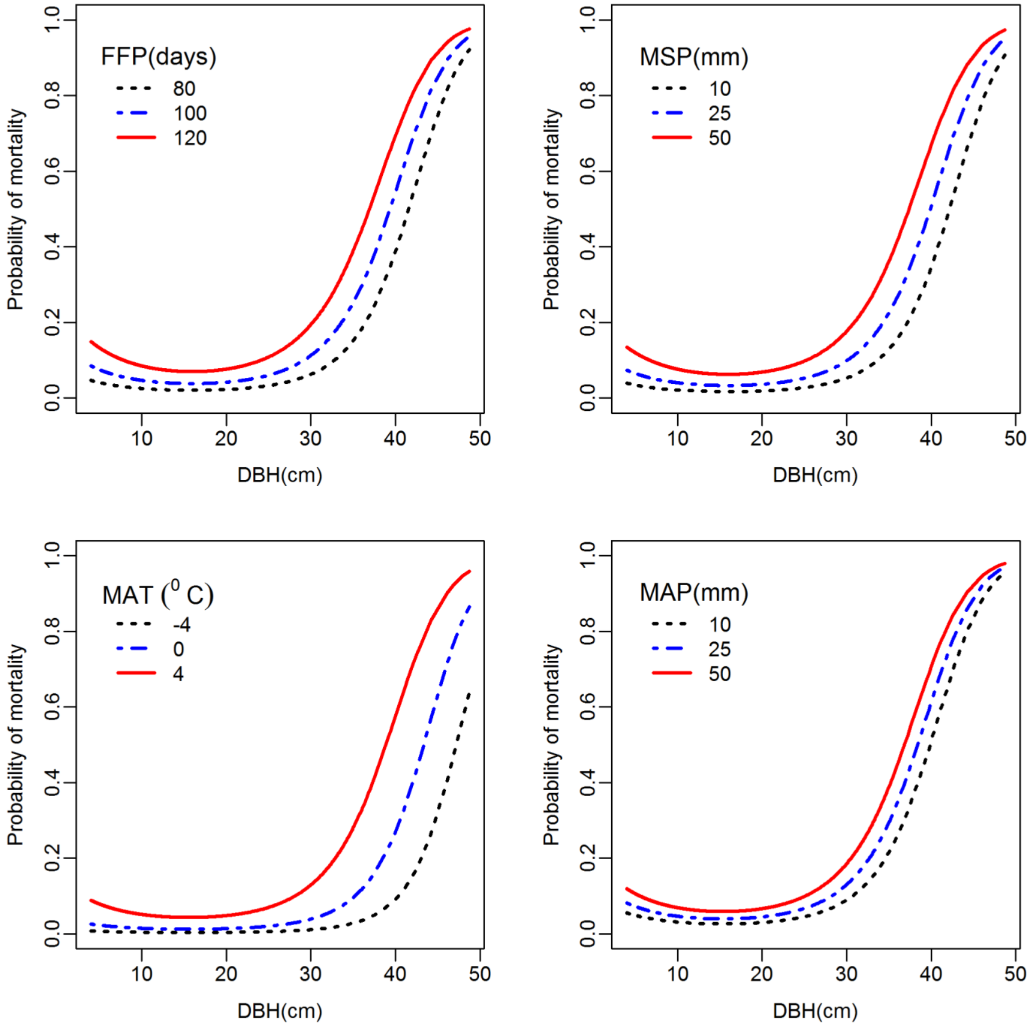

Figure 3.13. Predicted mortality across DBH under different climatic conditions- Frost free period (FFP), Mean summer precipitation (MSP), Mean annual temperature (MAT) and Mean annual precipitation (MAP).

3.3.5 Compatible diameter-height growth model

The compatible diameter-height growth model which was developed to examine how growth is allocated between diameter and height is presented in Table 3.11. The model includes the three basal area larger competition components (deciduous, pine and spruce/fir). A plot level random effect was included only for the intercept and the parameter associated with spruce/fir basal area larger (Equation 3.28, 3.29 and 3.30). Deciduous competition had no significant effect on diameter allocation but coniferous competition reduced growth allocation to diameter as well as the total competition of the stand ($InCRi$). The models (Equations 3.29 and 3.30) were significantly improved by inclusion of climate variables (Table 3.11). Allocation of growth to diameter was predicted for different climatic conditions and competition types. Spruce/fir competition decreases diameter growth allocation more rapidly than pine competition. CMI, MAT and MAP were associated with increases in diameter growth (Table 3.11 and Figure 3.14). The variance covariate included in the variance function was the $InCR$. The autocorrelation structure adopted was the CAR(1) which is similar to diameter and height growth model. The compatible diameter growth models are presented as:

[Eq. 3.28] Without climate:

$$\eta_{ijk} = (\beta_0 + b_{0i}) * \exp^{(-((\beta_1 \mathrm{DBH} + \beta_2 \mathrm{DecBAL} + (\beta_3 + b_{3i})\mathrm{SpruceFirBAL} + \beta_4\ \mathrm{PineBAL} + \beta_5 \mathrm{InCRi})))} + \varepsilon_{ijk}$$

[Eq. 3.29] With one climate variable:

$$\eta_{ijk} = (\beta_0 + b_{0i}) * \exp^{(-((\beta_1 \mathrm{DBH} + \beta_2 \mathrm{DecBAL} + (\beta_3 + b_{3i})\mathrm{SpruceFirBAL} + \beta_4\ \mathrm{PineBAL} + \beta_5 \mathrm{InCRi} + \beta_6 \mathrm{Climate})))} + \varepsilon_{ijk}$$

[Eq. 3.30] With two climate variable:

$$\eta_{ijk} =$$

$$(\beta_0 + b_{0i}) *$$

$$\exp^{\left(-\left(\left(\beta_1 \mathrm{DBH} + \beta_2 \mathrm{DecBAL} + (\beta_3 + b_{3i})\mathrm{SpruceFirBAL} + \beta_4\ \mathrm{PineBAL} + \beta_5 \mathrm{InCRi} + \beta_6 \mathrm{Climate}\mathbf{1} + \beta_7 \mathrm{Climate}\mathbf{2}\right)\right)\right)} + \varepsilon_{\mathrm{ijk}}$$

Where η is the proportionality constant which is the function of the tree's ability to put on diameter growth; $DecBAL, SpruceFirBAL, and\ PineBAL$ are basal area larger per hectare for deciduous, spruce and fir, and Pine; $\beta_{0,}$ $\beta_{1,}$ $\beta_{2,}$ $\beta_{3\ ,}$ β_4 are the fixed effects which are to be estimated; $b_{1i,}$ b_{3i} are plot level random effect.

Table 3.11. Parameter estimates for the compatible diameter - height growth models showing fixed effect estimates (standard error in parenthesis).

	Without climate	**MAT**	**MAP***	**CMI**	**MAT+ MAP****
β_0(intercept)	0.0108	0.0105	0.0082	0.0100	0.0084
	(0.0092)	(0.0097)	(0.0139)	(0.0097)	(0.0137)
β_1 (DBH)	-0.0103	-0.0104	-0.0099	-0.0101	-0.0100
	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)
β_2 (DecBAL)	0.0019 **ns**	0.0018 **ns**	0.0011 **ns**	0.0010 **ns**	0.0011**ns**
	(0.0001)	(0.0002)	(0.0002)	(0.0002)	(0.0002)
β_3 (SpruceFrirBAL)	0.0048	0.0049	0.0050	0.0049	0.0050
	(0.0001)	(0.0003)	(0.0004)	(0.0003)	(0.0001)
β_4 (PineBAL)	0.0007	0.0010	0.0013	0.0012	0.0014
	(0.003)	(0.0001)	(0.0001)	(0.0001)	(0.0001)
β_5 *(InCRi)*	0.0465	0.0563	0.0455	0.0437	0.0483
	(0.0002)	(0.0021)	(0.0022)	(0.0022)	(0.0023)
β_6 *(Climate1)*		-0.0235	-0.0005	-0.0039	-0.0067
		(0.0010)	(0.0001)	(0.0001)	(0.0012)
β_7 *(Climate 2)*					-0.0004
					(0.0001)
AIC	-1400705	-1400791	**-1400891**	-1400869	**-1400894**
BIC	-1400613	-1400690	**-1400790**	-1400768	**-1400783**

ns= not significant; *best single climate model; **best double climate model

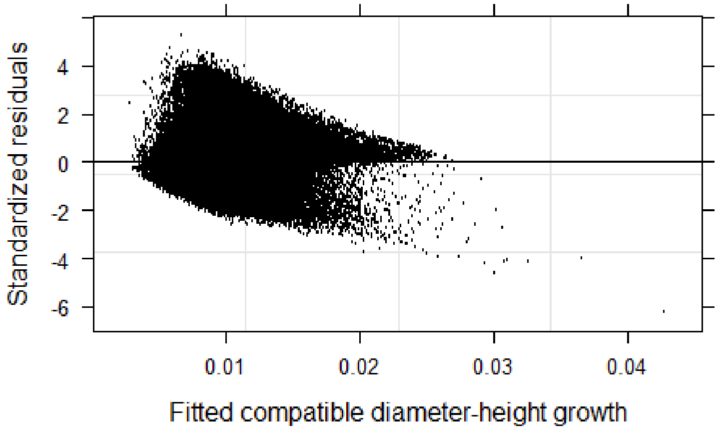

Figure 3.14. Plot of residuals for the best compatible diameter-height growth model.

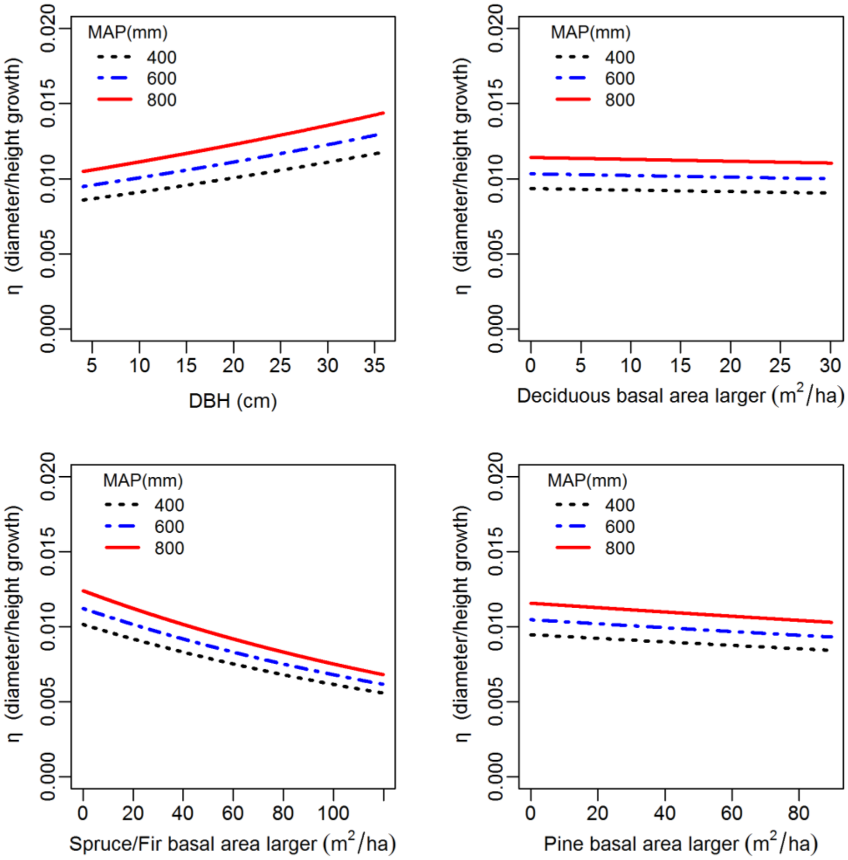

Figure 3.15. Predicted compatible diameter-height growth across the three competitor types - deciduous, spruce/fir and pine basal area per hectare.

3.3.6 Compatible diameter-volume growth model

The diameter – volume growth relationship was affected by DBH, deciduous and coniferous competition and climate variables which includes MAT, MAP and CMI but more strongly affected by CMI. Trees allocate less growth to diameter with an increase in deciduous, spruce/fir and pine competition, while more growth is allocated to diameter with an increase in MAT, MAP and CMI. The developed model is similar to Equations 3.28, 3.29 and 3.30 with the same predictor variables and modelling procedures. Random effects were included for intercept and spruce/fir basal area larger. Residuals for the best model (model with inclusion of CMI) are shown in Figure 3.16.

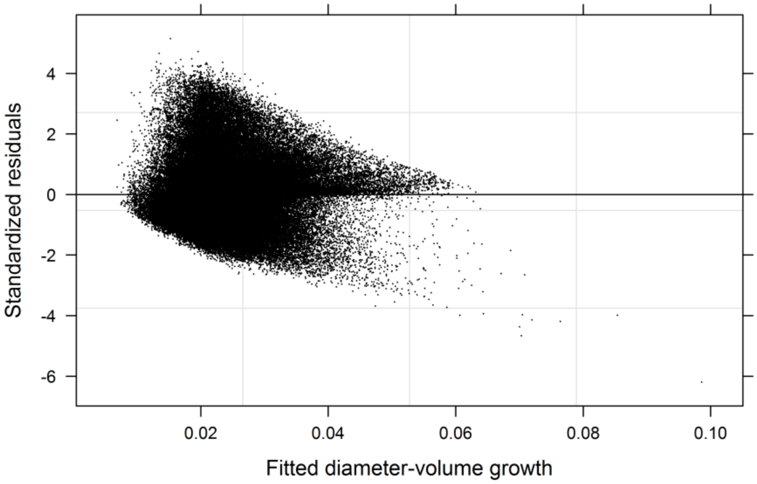

Figure 3.16. Plot of residual for the best compatible diameter-volume growth model.

Table 3.12. Parameter estimates for compatible diameter-volume growth models showing fixed effect estimates (standard error in parenthesis).

	Without climate	**MAT**	**MAP**	**CMI***	**MAT+ MAP**
β_0(intercept)	0.0281 (0.0004)	0.0277 (0.0004)	0.0220 (0.0005)	0.0260 (0.0059)	0.0221 (0.0058)
β_1 (DBH)	-0.0065(0.0006)	-0.0066 (0.0005)	-0.0062 (0.0006)	-0.0064(0.0001)	-0.0062 (0.0006)
β_2 (DecBAL)	0.0020 (0.0006)	0.0019 (0.0006)	0.0012 (0.0006)	0.0010 (0.0002)	0.0013 (0.0006)
β_3 (SpruceFrirBAL)	0.0056 (0.0001)	0.0056 (0.0001)	0.0057 (0.0001)	0.0056 (0.0001)	0.0057 (0.0001)
β_4 (PineBAL)	0.0013 (0.0002)	0.0015 (0.0002)	0.0018 (0.0002)	0.0018 (0.0001)	0.0019 (0.0002)
β_5 *(InCRi)*	0.0619 (0.0067)	0.0695 (0.0068)	0.0615 (0.0067)	0.0597 (0.0029)	0.0623 (0.0016)
β_6 *(Climate1)*		-0.0179 (0.0023)	-0.0004 (0.0001)	-0.0041(0.0001)	-0.0019**ns** (0.0028)
β_7 *(Climate 2)*					-0.0004 (0.0001)
AIC	-1102900	-1102953	-1103058	**-1103083**	-1103056
BIC	-1102809	-1102852	-1102956	**-1102981**	-1102944

ns= not significant; *best single climate model; **best double climate model

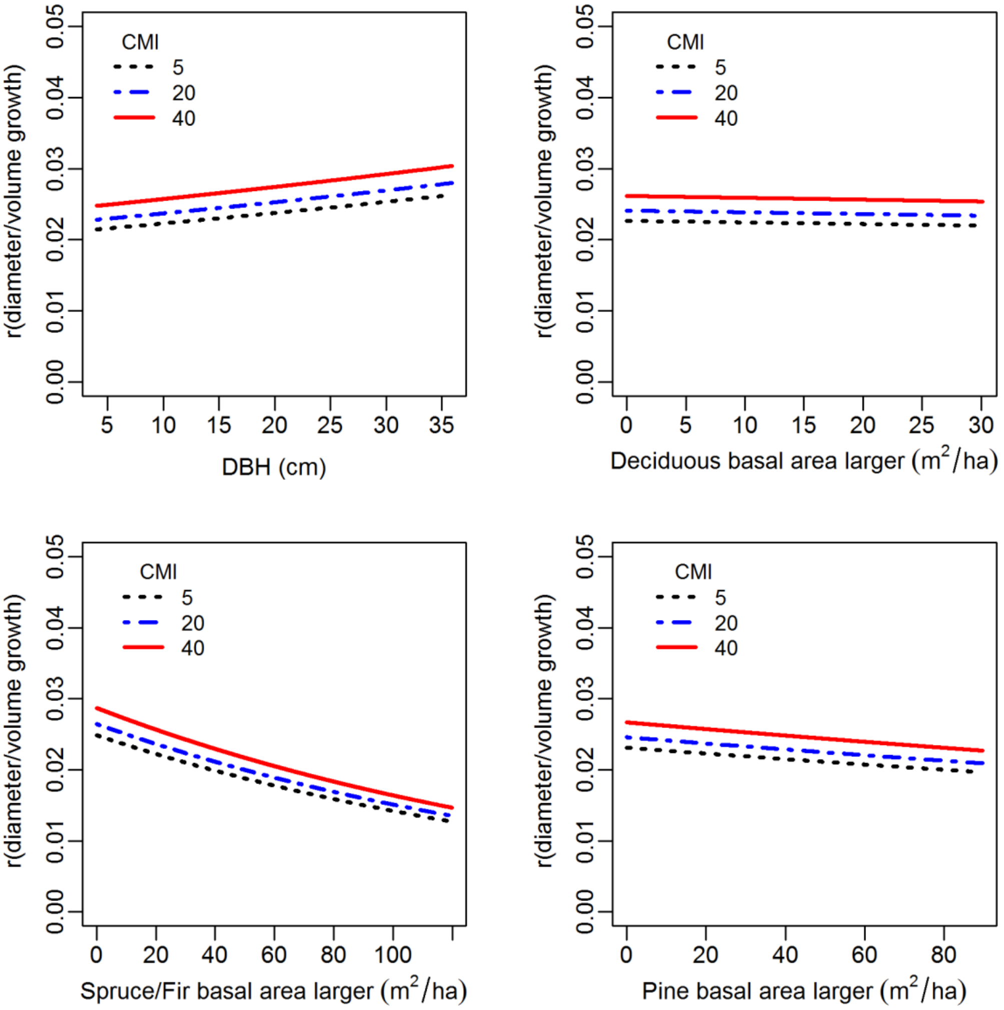

Figure 3.17. Predicted compatible diameter-volume growth for varying climate moisture index (CMI) across DBH and three competition types (deciduous, spruce/fir and pine).

3.3.7 Comparison between non compatible diameter growth model and modified compatible diameter growth models

The non compatible diameter model (Equation 3.19) was compared with modified MCDG (Equation 3.17) and MCDV (Equation 3.18) to ascertain the best method for developing diameter growth models. Comparison was done using the fixed effect estimates similar to

MGM together with the validation dataset. The non-compatible diameter growth model which is fitted directly is a better model (lower ME, MAE, RMSE and RE) for estimating diameter growth (lower ME, MAE, RMSE and RE values) than the modified compatible model fitted using the compatible diameter-height growth model. Results in Table 3.13 shows that the non compatible model had the lowest error (ME=0.022, RMSE=0.067) while the modified compatible diameter-volume model gave the highest error values (ME=0.103, RMSE=0.135).

Table 3.13. Model performance of non compatible diameter and modified compatible diameter growth model.

	ME	MAE	RMSE	RE (%)
Non compatible diameter	0.0222	0.0493	0.0674	39.19
Modified compatible diameter-height	0.0629	0.0599	0.0805	49.01
Modified compatible diameter-volume	0.1034	0.1011	0.1349	54.04

3.4 Discussion

3.4.1 Growth functions

Diameter growth, height growth, mortality and compatible growth functions are important components of an individual tree growth model like MGM. The NLME adoption in this study has been proven to improve model performance especially when dealing with hierarchical data with repeated measurements (Adame et al. 2008; Xu et al. 2014). Models developed in this study have a high predictive ability as reflected in validation results. The important predictor variables required by MGM were included with the addition of climate variables not previously used in MGM. Due to model form, variance functions for diameter and height growth models were best modelled when DImax and HImax were included as covariates in the variance function. Autocorrelation structure was also needed in all growth models to account for dependence among within-group errors (Pinheiro and Bates 2000).

3.4.2 Competition impacts on growth and mortality

Competition is often considered as a major factor affecting growth, and in this study, basal area larger was selected as the major predictor variable in both the diameter and height growth models. It has been shown to be a good competition index in models currently used in MGM for other boreal species including trembling aspen, white spruce, lodgepole pine, and jack pine (Bokalo 2012). However, basal area larger is regarded as a measure of one-sided competition which captures the effect of only larger trees and ignores competition from trees of the same size or smaller. Basal area larger was separated into deciduous, coniferous and spruce and fir basal area larger due to the fact that competition from each of these has different effects on spruce growth.

One –sided (asymmetric) competition captures the competitive advantage of larger trees over smaller trees. In this case smaller trees are assumed to have little effect on the growth and mortality of the larger trees. Interestingly, two sided competition indices like stand basal area (BA) and stand density index (SDI) have been reported to have a similar effect as basal area larger (Zhang et al. 2015). Basal area larger has been commonly used as a measure of competition (Quicke et al. 1994; Pokharel and Dech 2012) where it has provided a strong estimate of competition.

Results from this study indicate that competition accounts for a substantial amount of the variation in the diameter growth, height growth, and mortality of black spruce. Deciduous and coniferous competitions have positive and negative effects on spruce growth, respectively. Generally, deciduous trees are known to drop their leaves in the fall and spring season, and this provides an opportunity for black spruce to grow due to the increase in sunlight during those periods with less competition for water and nutrient (Constabel and Lieffers 1996). Aspen has been reported to have a positive effect on DBH and height of black spruce when the proportion of aspen is between 0% to 41% of the total stand basal area (Lēgarē et al. 2004), leading to the assumption that both species use different niches. Aspen can also enhance soil fertility by promoting nutrient availability and height growth of black spruce (Brais et al. 1995; Paré and Bergeron 1996; Lēgarē et al. 2004). In addition, the presence of aspen may be indicative of soils with higher nutrient availability or faster nutrient cycling. My results further support management of black spruce in mixedwood stands as these relationships can lead to overyielding which has also been observed in mixed stands of white spruce and trembling aspen (Kabzems et al. 2007, 2016).

Unlike deciduous, coniferous trees shade the black spruce throughout the year. The dense crown of conifers like spruce can be very detrimental to growth of other tree species including black spruce by intercepting photosynthetically active radiation and water (Constabel and Lieffers 1996). My results also show that black spruce growth was more strongly influenced by spruce and fir competition than pine competition. This might be resulting from higher crown density (and light interception) by spruce and fir species and is also likely related to strong niche overlap due to similarity in resource requirements (nutrient, water, light, space), and, consequently more intense competition. On the other hand, both deciduous and coniferous competition increased spruce mortality. Pine competition has the strongest effects on mortality in Equation 3.26, followed by deciduous competition and then spruce/fir competition. This might be due to the fact that pine and deciduous competitors tend to be taller so their combined effect is greater per unit basal area than spruce/fir competitors. In addition, pure black spruce stands are commonly wet, poor sites with generally slow growth and hence competition is gradual and results in less mortality. As mentioned previously, deciduous species drop their leaves during the fall and winter and this might be the reason while they have a weaker influence on mortality than pine. Cortini et al. (2017) also report that survival of black spruce was more strongly reduced by deciduous competition than spruce/fir competition.

3.4.3 Climate impacts on growth and mortality

Climate change has been found to have an influence on the growth of black spruce (Gamache and Payette 2004; Johnstone et al. 2010; Girardin et al. 2016). My results indicate that including climate variables improved performance of growth and mortality functions. Including both MAT and MAP in the model gave the best diameter and height growth models. Results show that MAT was more strongly related to diameter growth and had a positive effect while CMI was more strongly related to height and had a negative impact. Other studies have also indicated that diameter growth is strongly affected by temperature (Beedlow et al. 2013; Gennaretti et al. 2014; Manso 2015). This positive relationship was suggested to be a result of the increase in growing season (FFP) which is associated with high temperatures (Rossi et al. 2014) and increased carbon assimilation

(Ueyama et al. 2015). Interestingly, the current study show that since black spruce habitat is characterized by moist, wet soils and peatland (Iwata et al. 2012), an increase in soil water (CMI) in these already wet soils may be detrimental to growth. On the other hand, CMD was positively related to height growth and negatively related to diameter growth. This may reflect shifts in growth allocation to height when black spruce stands become drier, trees will allocate more growth to height than diameter. However, precipitation in the summer (MSP) was shown to be important in increasing diameter growth, while summer heat moisture index (SHM) was negatively related to diameter growth. This indicates that an increase in soil water availability in the summer is important for diameter growth even though an increase in moisture availability annually (CMI, MAP) shows a negative relationship.

The mortality functions without climate show a negative coefficient for DBH and a positive coefficient for DBH^2 which indicates that trees have lower mortality when they are small in size, and the rate of mortality becomes stable at a point and later increases for larger trees. This explanation has also been reported in survival models for species like white spruce, trembling aspen, and lodgepole pine where survival increases for smaller tree size and decreases for larger tree size (Yao et al. 2001; Cortini et al. 2017). Both mortality and survival results can easily be compared because they are directly opposite each other. Furthermore, this relationship was affected by the inclusion of climate in the model as climate variables significantly improved the model (Table 3.8). Increases in CMI result in decreased mortality. Cortini et al. (2017) also reported that increases in CMI were associated with increased survival of black spruce. Temperature and precipitation can also have indirect effects on mortality by increasing growth of competitors. The crown class of the subject tree in a stand is also likely to influence how the tree will be affected by competition and hence climate. Increases in mean annual temperature and precipitation led to increased mortality of black spruce. Mean summer precipitation was more strongly related to mortality than the other climate variables. This was followed by mean annual temperature and summer heat moisture index. This is also supported by the result of the height growth functions where summer climatic conditions (SHM and MSP) positively increased height growth.

Including climate in growth and mortality functions improves the performance of models. When climate variables are not included in growth models like MGM, the implicit assumption is that the rate of tree growth observed when the data used to calibrate the model were collected will remain constant in the future (Crookston et al. 2008). Relying on long-term averages in the calculation of climate variables provides models that respond to regional differences in long-term climate. Further analysis evaluating effects of climate change and to build models that are responsive to changes needs to consider climatic conditions during individual growth intervals or annual time steps. In addition, inclusion of soil and related topographic information could help to further improve predictions of effects of climate change on tree growth in relation to site conditions. Some data limitations encountered in the course of this study were not under our control, and include: (1) minor differences in measurement protocols; and, (2) the small number of measurements per tree which made it difficult to include tree level random effects due to convergence issues.

3.4.4 Effect of competition and climate on growth allocation

(a) Diameter-height relationship: Examining the height-diameter relationship using the compatible diameter growth functions explains the allocation of growth to diameter and height under changing competition and climatic conditions. Larger trees allocate more growth to diameter than height since larger trees are also taller hence closer to the potential maximum height for the site. Spruce/fir competition had a strong effect on diameter – height growth allocation while the effect of pine competition was weak. Deciduous did not show any significant effect on the diameter-height growth relationship which might be due to the low mean deciduous density in this study (369 trees per hectare) since higher densities is expected to have some negative effect on diameter growth. The non-significant effect of deciduous might also be attributed to the fact that they drop their leaves in the fall season which results to slight increase in growing conditions (Constabel and Lieffers 1996), hence allocation of growth might be controlled by the consistent change in growing conditions (intense competition in spring and summer and reduced competition in winter and fall). Trees also increase in diameter growth to maintain their height-diameter ratio in order to avoid windthrow (Wonn and O’Hara 2001). Pine competition slightly reduced diameter growth allocation compared to spruce/fir competition which reduced it drastically. The spruce/fir competition effect on diameter growth might be due to poor site condition or cluster distribution associated with black spruce natural regeneration (Rossi et al. 2013) since reduction in diameter growth allocation is often associated with suppression (Rich et al. 1986).

The three climate variables (CMI, MAT and MAP) were positively related to diameter growth allocation over height growth but MAP was more related to diameter growth allocation than the others. i.e as precipitation increases, the tree allocates more growth to diameter compared to height. Climate moisture index (CMI) provides a measure of the availability of moisture in the long term across various locations. Sites with higher CMI will support more diameter growth. Soil water availability has been reported to positively influence productivity of black spruce stands (Girardin et al. 2016), especially because black spruce are naturally found in areas of high humidity (Viereck and Johnston 1990). This compatible relationship also shows that MAT is more strongly related to diameter growth as observed in the non-compatible diameter growth function. This may reflect the fact that black spruce occurs predominantly on wetter peatland sites, or in the understory of cool moist sites, and as a consequence, increases in temperature are not resulting in drought stress. Since appropriate and balanced allocation of growth to height and diameter are necessary for tree stability and maintenance of tree form (Wonn and O'Hara 2001), this result from compatible model suggests that when there is an increase in climate variables (MAT, CMI and MAP) preference of growth allocation is to diameter over height i.e diameter allocation increases in wetter conditions while height allocation in drier climatic conditions, since MAT does not necessarily mean lower soil water.

(b) Diameter-volume relationship: Volume growth allocation results from accumulation of photosynthate along the stems of woody plants which is referred to as secondary growth (Gennaretti et al. 2017). The allocation of growth to diameter over volume is similar to diameter- height growth allocation which indicate that biomass increase is associated to tree height growth allocation (Seki et al. 2012). Results shows that larger tree will allocate more growth to diameter to maintain the diameter-volume growth relationship since volume growth comprises both diameter and height growth. CMI was more related to diameter growth over volume growth allocation than MAT and MAP. This indicates that sites with higher CMI will support more diameter growth than volume growth (less biomass accumulation). Climate moisture index (CMI) provides a measure of the availability of moisture in the long term across various locations. This growth allocation suggest that under high CMI trees have reduction in height growth, hence reduction in volume. This reduction in height growth will likely increase allocation to diameter growth though higher CMI still has a negative effects on diameter growth as indicated by result of non-compatible diameter and height growth models in this study.

Results indicate that as tree increase in size they allocate more growth to diameter over height or volume to create some stability in the tree which might be due to bending strain in base of trees which prevent them from breaking or susceptible to wind damage (Gartner 1995). Trees that are not thickened at the base (low cambial activity at the base) may allocate more growth to diameter to prevent breakage and maintain a stable height-diameter ratio.

3.4.6 Inclusion of compatibility in growth models

Height-diameter relationships are expected to vary due to changes in environmental conditions including competition (Kohyama 1996; Nunifu 2009) and climate (Wang et al. 2006; Banin et al. 2012). In MGM, height growth of individual trees is estimated using the SI functions for the particular species together with growth modifiers for effects of competitors. Diameter growth is then predicted using compatible diameter growth functions as shown in Equation 3.17. In this study, the same process used by MGM was followed and results revealed that diameter growth predicted from using compatible model had larger bias than the non-compatible model (Equation 3.19). Compatibility in growth and yield models can place constraints on the system of equation which may reduce the accuracy of the model (Ochi and Cao 2003) and it is therefore better to use non compatible diameter growth than compatible ones. Further analysis needs to consider effects of climatic conditions during individual growth intervals or annual time steps and should also consider inclusion of measures of potential stand productivity.

3.5 Conclusion

Improving the performance of growth functions is necessary to provide reliable stand projections and help in making better management decisions by forest owners and forest companies. The MGM is an operational growth model (with several sub models) that require to be updated inother to improve performance and range of applicability. Competition and some climate were major significant predictors in the sub models developed in this study. Although, deciduous competition covered a smaller range of densities than spruce/fir and pine, it was found to positively influence growth which might also be due to facilitation and niche separation between black spruce and deciduous species. Coniferous competition had negative effects on black spruce growth with spruce/fir competition having a stronger impact than pine. This study supports the inclusion of climate variables in growth and mortality functions. CMI and MAP negatively affected diameter and height while MAT affected them positively. Summer precipitation had a strong positive influence on growth and mortality whereas annual precipitation negatively influenced growth which indicates that seasonal precipitation can have varying effects on black spruce growth. Competition had a similar effects on diameter-height growth relationship and diameter-volume growth. Although, compatibility of submodels in growth and yield models like MGM helps to ensure predictions are consistent and reliable, results from this study suggest that diameter growth models developed in this manner can be biased and were therefore weaker than the non-compatible models.

Chapter 4: An evaluation of validation procedures: A case study using black spruce (*Picea mariana* (Mill.) BSP.) and the Mixedwood Growth Model (MGM).

4.1 Introduction

It is important that a model is evaluated and validated to demonstrate that it provides reasonable estimates and predictions before it is used. While forest growth and yield modelling has been underway for several decades (Vanclay and Skovsgaard 1997; Shifley et al. 2017) there is ongoing discussion regarding how to conduct a proper validation (Huang et al. 2003). Model validation is an important part of evaluating a model and often done continuously throughout the development and use of a model (Soares et al. 1995; Pretzsch 2002). As noted by Huang et al. (2003), the validation of growth and yield models like Mixedwood Growth Model (MGM), is often complicated due to the fact that the submodels inside the model were developed using different approaches. For example MGM has individual components like the growth functions, mortality functions, maximum-size density functions and also the compatible growth model that link height and diameter together (Bokalo et al. 2013).

The Mixedwood Growth Model has been developed as a tool to improve management decisions for pure and mixed stands in the western Canadian boreal forest (Bokalo et al. 2013). The model is able to forecast growth and yield for several western boreal tree species including trembling aspen (*Populus* tremuloides Michx.), white spruce (*Picea glauca*(Moench) Voss), lodgepole pine (*Pinus contorta* var. latifolia Engelm.), jack pine (*Pinus banksiana*Lamb.), and black spruce (*Picea mariana* (Mill.) BSP.) (Nunifu 2009; Bokalo et al. 2013; Strimbu et al. 2017). Validation of MGM is usually done to assess the model performance when new growth and mortality functions are incorporated into the model. In most cases validation is done for dominant species at provincial jurisdiction, and for each broad cover group. This is to ensure that all components of the model can adequately predict growth with high accuracy. Validation also identifies weaknesses in the model in order to guide ongoing refinement. Consequently, there is need to assess performance of MGM following implementation of the new black spruce growth (presented earlier in this thesis), mortality (Cortini et al. 2017) and maximum size density functions (Comeau et al. in preparation) which have been added to the model .

Validating the overall performance of a model is regarded as more important than the performance of the individual components since stand projections or forecasts are conducted using the overall system (Huang et al. 2003). Graphical exploration of model predictions is often regarded as a good way to assess the overall model (Frey and Patil 2002; Huang et al. 2003). On the other hand, when individual components are poorly developed it might have an impact on the overall system. Once a model is fitted, an assessment of its validity using an independent data set is needed to see if the quality of the fit reflects the quality of predictions.

Traditionally, modellers have split datasets into two parts – a calibration data set and a validation data. Although this approach is generally accepted, in reality, one tends to find that many models behave undesirably in application. However, fitting and validation datasets are not independent and therefore, the purpose of reserving independent data might not have significant effects on the validity of the model (Davis and Johnson 1987). Consequently, Huang et al. (2003) suggested that forest modellers should look for a more balanced, reliable method for validation. Model building will require as much data as possible to simulate the process in question. Due to the scarcity of data, it is important to evaluate the need to split data as this might have an influence on the performance of the model. Modellers are posed with the decision of whether to split a small data set or not. Since the validation data is not independent, it might be regarded as a waste of important data that would have contributed to improving model performance. On the other hand, it is also unclear whether a smaller calibration dataset after splitting might produce a weaker model than the full data set. Since it affects the size of the calibration dataset, the proportion of splitting will strongly determine model performance. Since there is no 'right' way to validate a model, modellers are faced with questions like how much data should be reserved for validation, how to sample datasets for validation and what validation metrics to use. This study will examine the use of 90% and 50% of the dataset in model fitting with the balance used in validation.

Objectives

The objectives of this part of my study are to:

(1) Evaluate the effects of reserving different proportions of plot data for validation, and

(2) Validate MGM for black spruce using stand parameters which includes volume, basal area, DBH, height, density and top height.

4.2 Materials and methods

4.2.1 Data

Repeated measurement data were made available from government and companies across various provinces in western Canada and Alaska. The Alberta data was from permanent sample plots (PSP) assembled in the Provincial Growth and Yield Initiative (PGYI). Other provinces including Saskatchewan, northeastern British Columbia and Manitoba provided PSP data (Figure 4.1). Part of this data was utilized in development of mortality functions for western boreal tree species (Cortini et al. 2017). A plot level validation dataset was not reserved during the mortality model development phase. However, during development of black spruce growth functions validation datasets were created by removing a random selection of plots from the model-fitting dataset.

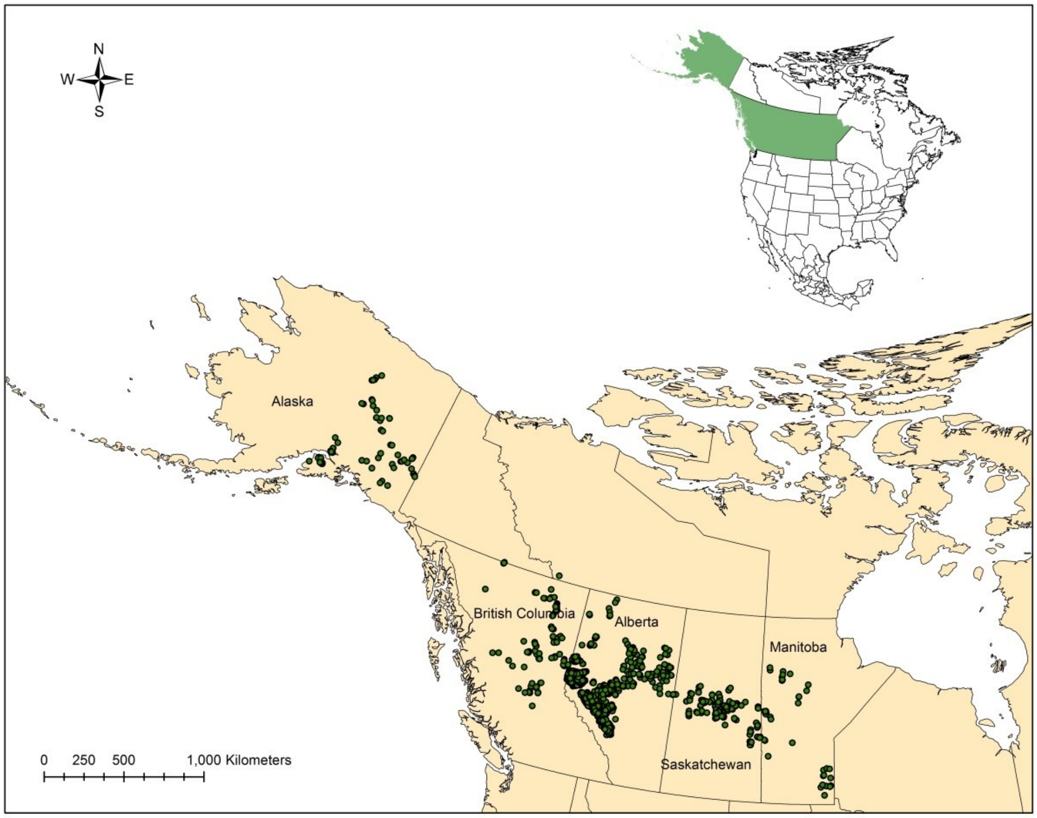

Figure 4.1. Location of plots across the different provinces and Alaska.

4.2.2 Effects of reserving different proportions of plot data for validation.

To address objective one, all the data collected across the four Canadian provinces and Alaska were used (Figure 4.1). The effect of reserving data for validation was tested using some black spruce diameter increment models. The procedures followed to address this part of my study include bootstrapping and diagnostic testing.

4.2.2.1 Bootstrapping

The iterative process (bootstrapping) involves splitting dataset, model development and validation of model. The iterative process was carried out 1000 times (McRoberts et al. 2011). Each process involves repetition of three steps which are descripted in detail below (4.2.2.1a - 4.2.2.1c).

The estimate of the mean $\hat{u}_{boot}$, and its estimates of bias n_{boot} and variance Var_{boot} of the 1000th bootstrap sample were obtained as;

[Eq. 4.1] $$\hat{u}_{boot} = \frac{1}{n_{boot}} \sum_{b=1}^{n_{boot}} \hat{u}_{boot}^{b} \ ,$$

[Eq. 4.2] $$Est.Bias_{boot}(\hat{u}) = \hat{u}_{boot} - \hat{u} \ ,$$

[Eq. 4.3] $$Est.Var_{boot}(\hat{u}) = \frac{1}{n_{boot}-1} \sum_{b=1}^{n_{boot}} \left(\hat{u}_{boot}{}^{b} - \hat{u}\right)^{2}$$

where n_{boot} is the number of bootstrap samples (1000^{th} bootstrap).The estimate of the standard error was obtained as the square root of the variance estimate (Equation 4.3) (Efron and Tibshirani 1994; McRoberts et al. 2011).

4.2.2.1a Splitting ratio

Splitting the dataset was the first step in the bootstrap process. The dataset was first separated with 90% reserved for model fitting and 10% reserved for validation. A second model fitting dataset was created by randomly selecting 55.5% plots from the original 90% dataset (Figure 4.2) which is equivalent to 50% of the full dataset (100%). Having a 55.5% dataset which is a subset of the 90% dataset allowed for the evaluation of model performance resulting from data reduction. The model fitting datasets were used for model development while the validation datasets were used for validating the models. These splitting ratios are widely used in model validation (Huang et al. 2003).

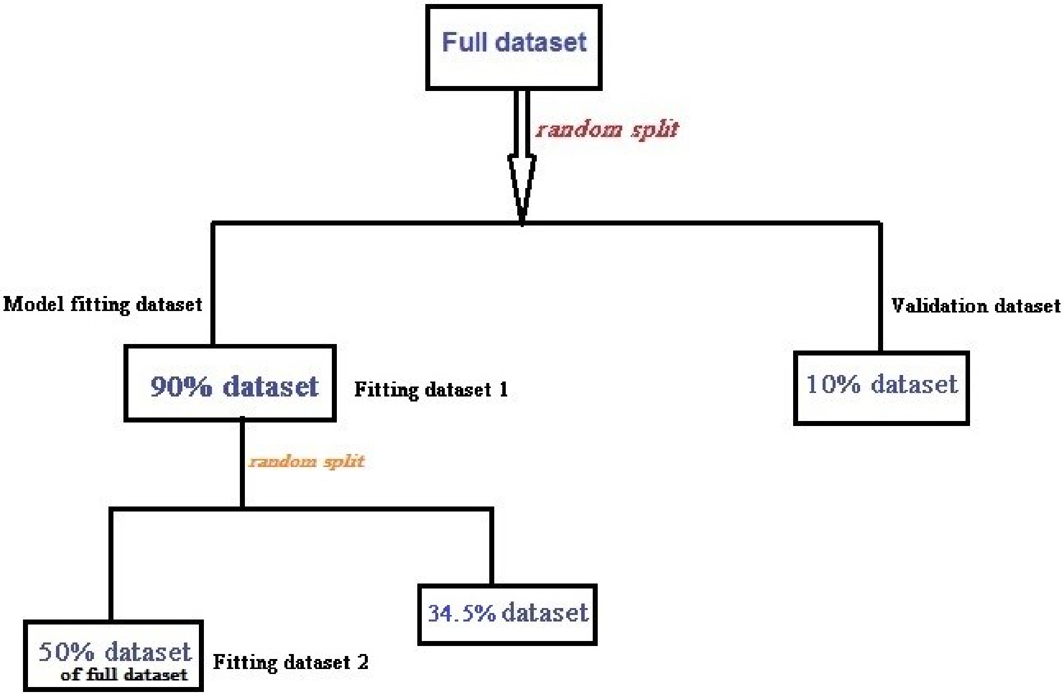

Figure 4.2. Procedures for splitting datasets

4.2.2.1b Model development

Eight diameter growth models (four different model forms) were developed using each of the calibration datasets developed after data splitting. All diameter growth models were fitted with three competition variables (deciduous, spruce/fir and pine) with and without climate variable (Mean annual temperature). The response variable was annual diameter increment. Each model was developed using both calibration datasets i.e. eight models developed with 90% and 50% datasets.

The eight models developed were:

First model form Equation 4.1 and 4.2

[Eq. 4.4]

$$\mathbf{DDBH\ incr_{ijk}} = DImax_{jk} * exp^{\left(-((\beta_0 + b_{0i}) + \beta_1 DecBAL + \beta_2 SpruceFirBAL\ +\ \beta_3 PineBAL)\right)} + \varepsilon_{ijk}$$

[Eq. 4.5]

$$\mathbf{DDBH\ incr_{ijk}} = DImax_{jk} * exp^{\left(-((\beta_0 + b_{0i}) + \beta_1 DecBAL + \beta_2 SpruceFirBAL\ +\ \beta_3 PineBAL + \beta_4 MAT\ )\right)} + \varepsilon_{ijk}$$

Second model form Equation 4.3 and 4.4

[Eq. 4.6] $\mathbf{DBH\ incr_{ijk}} = htinc_{jk} * exp^{\left(-((\beta_0 + b_{0i}) + \beta_1 DecBAL + \beta_2 SpruceFirBAL\ +\ \beta_3 PineBAL)\right)} + \varepsilon_{ijk}$

[Eq. 4.7] $\mathbf{DBH\ incr_{ijk}} = htinc_{jk} * exp^{\left(-((\beta_0 + b_{0i}) + \beta_1 DecBAL + \beta_2 SpruceFirBAL\ +\ \beta_3 PineBAL + \beta_4 MAT)\right)} + \varepsilon_{ijk}$

Third model form Equation 4.5 and 4.6

[Eq. 4.8] $\mathbf{DBH\ incr_{ijk}} = exp^{\left(-((\beta_0 + b_{0i}) + \beta_1 DecBAL + \beta_2 SpruceFirBAL\ +\ \beta_3 PineBAL)\right)} + \varepsilon_{ijk}$

[Eq. 4.9] $\mathbf{DBH\ incr_{ijk}} = exp^{\left(-((\beta_0 + b_{0i}) + \beta_1 DecBAL + \beta_2 SpruceFirBAL\ +\ \beta_3 PineBAL + \beta_4 MAT)\right)} + \varepsilon_{ijk}$

Fourth model form Equation 4.7 and 4.8

[Eq. 4.10] $\mathbf{DBH\ incr_{ijk}} = a * exp^{\left(-((\beta_0 + b_{0i}) + \beta_1 DecBAL + \beta_2 SpruceFirBAL\ +\ \beta_3 PineBAL)\right)} + \varepsilon_{ijk}$

[Eq. 4.11] $\mathbf{DBH\ incr_{ijk}} = a * exp^{\left(-((\beta_0 + b_{0i}) + \beta_1 DecBAL + \beta_2 SpruceFirBAL\ +\ \beta_3 PineBAL + \beta_4\ MAT)\right)} + \varepsilon_{ijk}$

where $DImax_{jk}$ is the maximum diameter increment for plot i at measurement k; $DecBAL,\ SpruceFirBAL,\ and\ PineBAL$ are basal area larger per hectare for deciduous, spruce and fir, and Pine; htinc is the individual tree height increment; β_0, β_1, β_2, β_3 and β_4 are the fixed effects which are to be estimated; b_0 is plot level random effect.

Variance structures were included for models as well as autocorrelation structure to account for repeated measurement (Pinheiro and Bates 2000).

4.2.2.1c Model validation

Model validation was the last step in the bootstrapping process. The developed models were validated using the reserved data set, i.e. 16 models developed with 90% and 50% datasets were validated with the 10% reserved data. Using the same validation dataset allowed for easy comparison of both set of split ratios.

The performance of the fixed effect parameters of the models on an independent dataset (10% reserved dataset) were evaluated using the following statistics: mean absolute error (MAE) and root mean square error (RMSE). They were estimated as presented below;

[Eq. 4.12] $$MAE = \frac{\Sigma\ |y_i - \hat{y}_i|}{n}$$

[Eq. 4.13] $$RMSE = \sqrt{\frac{\Sigma (y_i - \hat{y}_i)^2}{n}}$$

4.2.2.2 Diagnostic testing

Data generated from the 1000 iterative bootstrap process includes the estimates, biases and standard errors of the validation metrics (MAE and RMSE) for all models. The differences between models developed with 90% and 50% dataset were statistically tested. Three statistical test were used, namely: paired t-test (Rawlings 1988, Huang et al. 2003), Kolmogorov-Smirnov (KS) test (Stephens 1974; Huang et al. 2003) and Wilcoxon signed-rank test (Daniel 1995; Huang et al. 2003).

4.2.3 Validating MGM for black spruce

Functions developed for black spruce using the large data set as part of MGM recalibration were organized and the fixed effect parameters were coded into MGM since MGM requires only the fixed effect parameters (MGM, Bokalo et al. 2013). The growth functions (diameter, height, and compatible diameter) were developed in Chapter 2 of this thesis and are presented in Equations 4.14 and 4.15, and Table 4.1 below:

[Eq. 4.14] Diameter and height growth models:

$$\textbf{Diameter or height increment}_{\mathbf{ijk}} = \text{Max DBH or height increment}_{jk} * \exp^{(-((\beta_0 + b_{0i}) + (\beta_1 + b_{2i})\text{DecBAL} + (\beta_2 + b_{2i})\text{SpruceFirBAL} + \beta_3\text{PineBAL}))} + \varepsilon_{ijk}$$

[Eq. 4.15] Compatible diameter growth model:

$$\boldsymbol{\eta}_{\mathbf{ijk}} = (\beta_0 + b_{0i}) * \exp^{(-((\beta_1\text{DBH} + \beta_2\text{DecBAL} + (\beta_3 + b_{3i})\text{SpruceFirBAL} + \beta_4\text{ PineBAL} + \beta_5\text{InCR})))} + \varepsilon_{ijk}$$

Where η is the proportionality constant which is the function of the tree's ability to put on diameter growth; $DecBAL, SpruceFirBAL, and\ PineBAL$ are basal area larger per hectare for deciduous, spruce and fir, and Pine; $\beta_{0,}$ $\beta_{1,}$ $\beta_{2,}$ $\beta_{3\ ,}$ β_4 are the fixed effects which are to be estimated; $b_{1i,}$ $b_{2i.}$,b_{3i} are plot level random effect.

Table 4.1 Parameter estimates for the growth models showing fixed effect estimates (standard error in parenthesis).

Parameter	**Diameter growth model**	**Height growth model**	**Compatible diameter growth model**
β_0(intercept)	0.3844 (0.0075)	0.6935 (0.0094)	0.0108 (0.0092)
β_1 (DBH)			-0.0103 (0.0001)
β_2 (DecBAL)	-0.0100 (0.0012)	-0.0151 (0.0014)	0.0019 **ns** (0.0001)
β_3 (SpruceFrirBAL)	0.0243 (0.0006)	0.0140 (0.0005)	0.0048 (0.0001)
β_4 (PineBAL)	0.0030 (0.0002)	0.0018 (0.0003)	0.0007 (0.003)
β_5 *(InCR)*			0.0465 (0.0002)

ns= not significant

Mortality functions for black spruce developed by Cortini et al. 2017 and maximum density functions developed by Comeau et al. (in preparation) were also implemented in MGM.

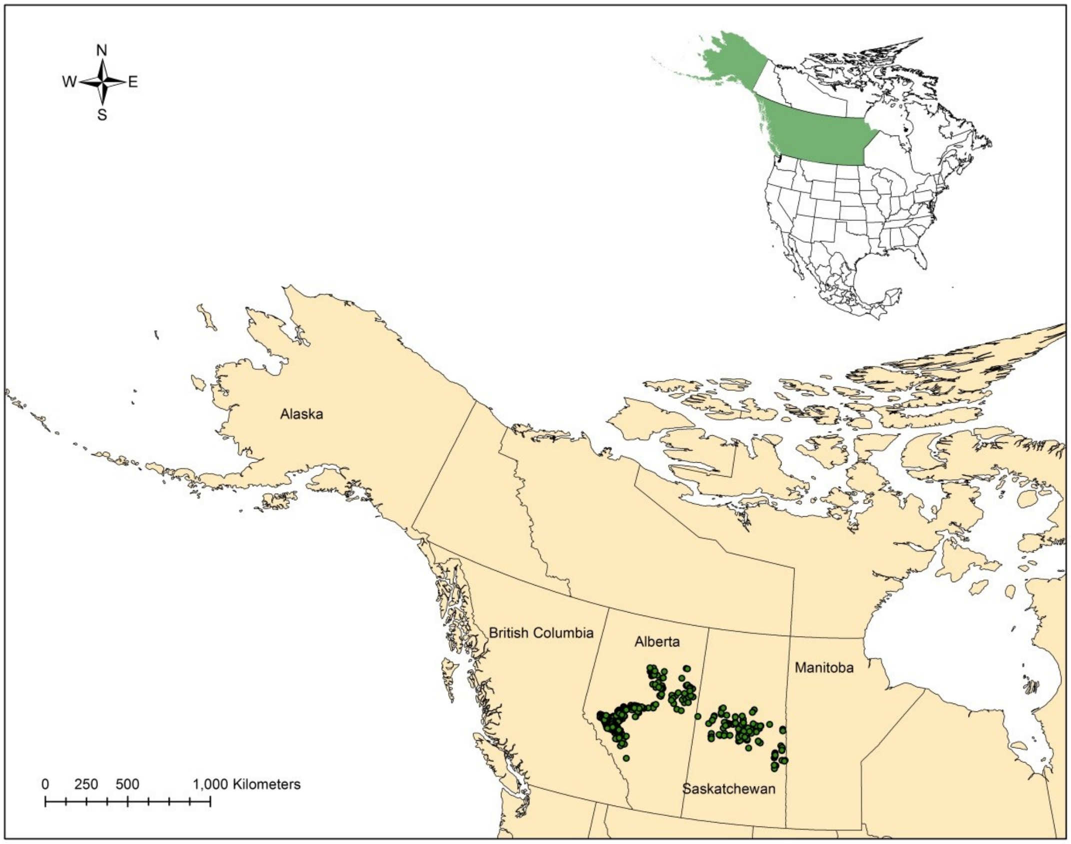

Figure 4.3. Location of MGM validation plots for Alberta and Saskatchewan.

Validation of MGM as a system was done using Alberta PGYI and Saskatchewan PSP data used in fitting the mortality and maximum density functions (Figure 4.3). The procedures used in this validation follow already defined methods and evaluation metrics reported in previous studies (Strimbu et al. 2017; Bokalo et al. 2013) except for the fact that the data used here were also a part of the model building dataset. This validation used the first plot measurement to initialize MGM and then the tree-list was projected to the final re-measurement where observed stand conditions were evaluated against the MGM predictions. The use of only the final measurement for validation provided the longest possible growth interval and also eliminated autocorrelation problems that can result from using repeated measurements from the same stand.

Validation of the MGM was done at the stand level for stand volume (m^3/ha), stand basal area (m^2/ha), average DBH (cm), average height (m), top height (m) and stand density (stems/ha) outputs for deciduous and conifer components. Top height was defined as the average height of the thickest 100 stems/ha of each species (Strimbu et al. 2017). Basal area, density, and top height are readily measurable in the field, and are useful for tracking stand performance against the model. Average height and DBH are additional simple metrics of tree size. There were no removals simulated over the projection periods (or identified in the data) and ingress was not included (in either the model or the validation data).

Both graphical methods and statistical metrics were used to assess the validity of the predictions. As graphical measures, plots of the observed (Y) versus predicted ($\hat{Y}$), with a Y= $\hat{Y}$ line representing the perfect fit, were used to evaluate the goodness of fit and identify any model biases (Bokalo et al. 2013). Average mean bias (AMB), relative model bias in percentage (RMB) and efficiency (EF) were calculated and used as statistical metrics of model validity (Vanclay and Skovsgaard 1997; Bokalo et al. 2013; Strimbu et al. 2017). Average mean bias (AMB) provides a measure of the average residual errors and was calculated using the formula:

[Eq. 4.16] $$AMB = \frac{1}{n}\sum\left(Y_i - \hat{Y}_i\right)$$

where Y_i, $\hat{Y}_i$ are observed and predicted values respectively, and n is the total number of observations used in fitting the model. A model with an AMB of 0 would indicate no bias.

The relative model bias (RMB), expressed as a percentage was used to provide an indication of the magnitude of the AMB by relating AMB to the observed mean estimator ($\overline{Y}$) (Strimbu et al. 2017). It is calculated using the formula:

[Eq. 4.17]
$$RMB = (\tfrac{1}{n}\sum\left(Y_i - \hat{Y}_i\right)/\overline{Y}) \times 100$$

where $\overline{Y}$ is the average of the observed values. These two metrics considered together, AMB and RMB, can provide the end user with an overall assessment of bias.

Efficiency (EF) relates the model predictions to the observed data and it is similar to the coefficient of determination (R^2). An EF value of 1 indicates a perfect model while an EF value of less than 0 indicates a poorer fit. Lower EF value reflect poor precision in individual errors which is a valuable information used to assess the predictive ability of a model. Efficiency was computed using the formula:

[Eq. 4.18]
$$EF = 1 - \frac{\sum(Y_i - \hat{Y}_i)^2}{\sum(Y_i - \overline{Y}_i)^2}$$

where Y_i, $\hat{Y}_i$ and $\overline{Y}$ are as shown above.

4.3 Results

4.3.1 Comparing model performance based on 90% and 50% dataset

As reported by McRoberts et al. (2011), one thousand bootstrap samples were sufficient to generate the means estimates for both dataset. This is evident in the estimates (mean, bias and standard error) shown in Figure 4.4 and 4.5 and Table 4.2. The values for both datasets were similar since they were based on the average of 1,000 samples and MAE and RMSE were generally lower for 90% dataset except for model 3 (Figure 4.4 and 4.5).

Furthermore, including MAT in the model did not always reduce the error (lower MAE and RMSE) as revealed in the first model form (model 1 and 2) and fourth model form (model 7 and 8). Interestingly, with the inclusion of MAT, the differences between the two datasets is lower except in the third model form (model 5 and 6).

Across all model forms (Table 4.2), the second model form had the lowest MAE and RMSE values for both datasets. The lowest MAE for the 90% dataset was 0.0526 (model 4) and 0. 0533 (model 4) for 50%. These were followed closely by model 3 with 0.0532 for 90% (MAE) and 0.0532 for 505 (MAE). The highest MAE and RMSE were found in the fourth model form with highest MAE values (0.0643- model 8; 0.0617-model 7) for 90% dataset while the 50% dataset was 0.0631 for model 8 and 0.0626 for model 7.

Table 4.2 Estimates of validation metrics from bootstrapping for the two datasets.

		90% dataset						50% dataset					
		MAE			RMSE			MAE			RMSE		
Eqn	Model	Mean	bias	SE	Mean	bias	SE	Mean	bias	SE	Mean	bias	SE
4.4	1	0.0591	0.0105	0.0005	0.0766	0.0141	0.0006	0.0593	0.0105	0.0017	0.0767	0.0143	0.0020
4.5	2	0.0596	0.0110	0.0005	0.0772	0.0153	0.0007	0.0596	0.0113	0.0015	0.0771	0.0160	0.0018
4.6	3	0.0532	0.0010	0.0003	0.0725	0.0015	0.0006	0.0533	0.0009	0.0004	0.0727	0.0014	0.0006
4.7	4	0.0526	0.0013	0.0003	0.0720	0.0019	0.0006	0.0532	0.0008	0.0004	0.0725	0.0015	0.0006
4.8	5	0.0577	0.0002	0.0003	0.0761	-0.0005	0.0007	0.0581	0.0003	0.0013	0.0765	-0.0003	0.0011
4.9	6	0.0571	0.0009	0.0004	0.0750	0.0004	0.0006	0.0579	0.0010	0.0012	0.0761	0.0002	0.0010
4.10	7	0.0617	0.0004	0.0004	0.0790	-0.0007	0.0006	0.0626	0.0001	0.0016	0.080	-0.0009	0.0013
4.11	8	0.0634	0.0026	0.0005	0.0804	0.0020	0.0007	0.0631	0.0039	0.0024	0.0799	0.0035	0.0022

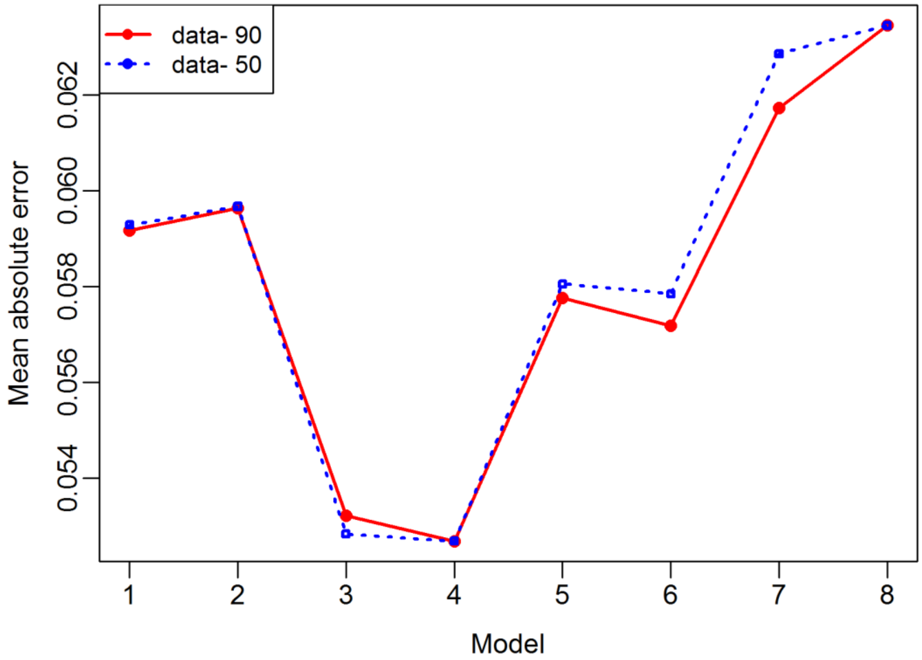

Figure 4.4. Comparing 90% and 50% datasets based on MAE values

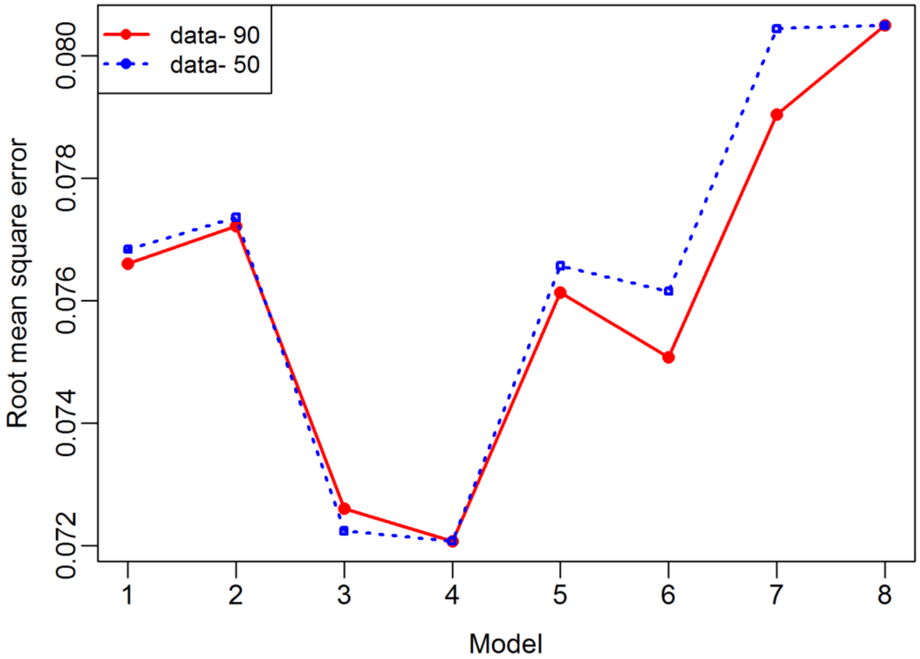

Figure 4.5. Comparing 90% and 50% datasets based on RMSE values

Results from the test (paired t, Kolmorogov Snirnov (KS) and Wilcoxon) showed that the difference between the models developed with 90% and 50% datasets were not significant at 0.05 prob level. Results from both MAE and RMSE were similar (Table 4.2).

Table 4.3 Results of different tests on the validation metrics.

Test	MAE		RMSE	
	Statistics	p-value	Statistics	p-value
Paired t	-2.0103	0.0843	-1.4071	0.2022
KS	5	0.0781	7	0.1484
Wilcoxon	0.25	0.9801	0.125	0.9990

4.3.2 Validation of MGM

4.3.2.1 MGM Validation using Alberta dataset

Using the complete Alberta PGYI dataset, the validation results are shown in Table 4.4 while the scatterplots are presented in Figure 4.6 and 4.7. The RMB (%) values were low (below 5%) for conifer and deciduous components of DBH, height and top height. Volume was overestimated for conifer (-22.28%) and underestimated for deciduous (11.53%). Density was overestimated for conifer (-11.71%) and slightly overestimated for deciduous (-0.17%). Except for deciduous density, Efficiencies (EF) for the deciduous component are all greater than 0.75% while EF for conifer are above 0.80% except for stand volume (0.58%) and stand basal area (0.59%).

The validation results for only black spruce are presented in Table 4.5 and scatterplots in Figure 4.8 and 4.9. The RMB (%) were generally low for conifer except volume (-13.87%)

where there was overestimation of 15.47m^3/ha. Efficiency was also high for conifer (above 76%). On the other hand, RMB (%) was higher for deciduous ranging from -19.30 (DBH) to 31.57 (Density). The deciduous component is overestimated on average in volume (RMB=-18.94%), basal area (RMB=-5.34%), DBH (RMB=-19.31%), and height (RMB=-18.89%) while top height (RMB=20.06%) is underestimated. Efficiencies are high for volume, basal area and density, but lower for dbh, height, and top height.

Table 4.4 Means, ranges and standard deviation(SD) for observed and model fit statistics for selected conifer and deciduous variables based on simulations for 1154 Alberta PGYI PSP's using MGMvs 2017 A1 (Rev5712).

	Conifer							**Deciduous**						
	Observed				**Statistics of Model Fit**			**Observed**				**Statistics of Model Fit**		
Variable	**Mean**	**Min**	**Max**	**SD**	**AMB**	**RMB(%)**	**EF**	**Mean**	**Min**	**Max**	**SD**	**AMB**	**RMB(%)**	**EF**
Volume (m^3/ha)	140.74	0.05	618.58	132.28	-31.36	**-22.28**	0.58	120.22	0	646.93	127.89	13.86	**11.53**	0.86
BA (m^2/ha)	17.30	0.03	58.53	13.83	-2.88	**-16.64**	0.59	13.31	0	58.25	12.55	1.53	**11.50**	0.83
DBH (cm)	19.89	2.55	72.75	9.08	-0.08	-0.40	0.84	21.14	0.69	62.2	10.45	-0.79	-3.76	0.78
Height (m)	15.09	2.63	33.15	5.82	-0.15	-1.02	0.87	17.18	2	37.09	6.64	-0.64	-3.76	0.76
Density (sph)	720.66	0.00	12875	1162.98	-84.44	**-11.71**	0.80	251.00	0	3875	427.63	-1.79	-0.71	0.55
Top Height (m)	17.94	2.86	37.19	6.55	-0.21	-1.22	0.91	19.18	2	37.09	6.95	-0.87	-4.58	0.84

Table 4.5 Means, ranges and standard deviation(SD) for observed and model fit statistics for selected conifer and deciduous variables based on simulations for 139 Alberta PGYI PSP’s dominated by black spruce using MGMvs 2017 A1 (Rev5712).

	Conifer							**Deciduous**						
	Observed				**Statistics of Model Fit**			**Observed**				**Statistics of Model Fit**		
Variable	**Mean**	**Min**	**Max**	**SD**	**AMB**	**RMB(%)**	**EF**	**Mean**	**Min**	**Max**	**SD**	**AMB**	**RMB(%)**	**EF**
Volume (m^3/ha)	111.58	1.19	469.92	101.51	-15.47	**-13.86**	0.82	10.85	0.00	56.03	14.15	-2.05	**-18.94**	0.82
BA (m^2/ha)	17.91	0.35	53.24	13.60	-1.04	-5.82	0.77	1.64	0.00	8.10	2.00	-0.08	-5.34	0.83
DBH (cm)	15.03	2.81	27.40	5.03	-0.78	-5.24	0.84	16.22	0.7	34.35	9.20	-3.13	**-19.30**	0.63
Height (m)	11.92	2.92	21.59	3.74	-0.08	-0.69	0.90	13.02	2	20.1	5.28	-2.46	**-18.89**	0.39
Density (sph)	1403.39	24.69	11175	1848.03	-33.66	-2.39	0.79	21.54	0	1600	138.00	6.80	**31.57**	0.94
Top Height (m)	15.13	5.425	27.05	4.32	-0.37	-2.50	0.82	13.37	2	20.1	4.97	-2.46	**-18.40**	0.34

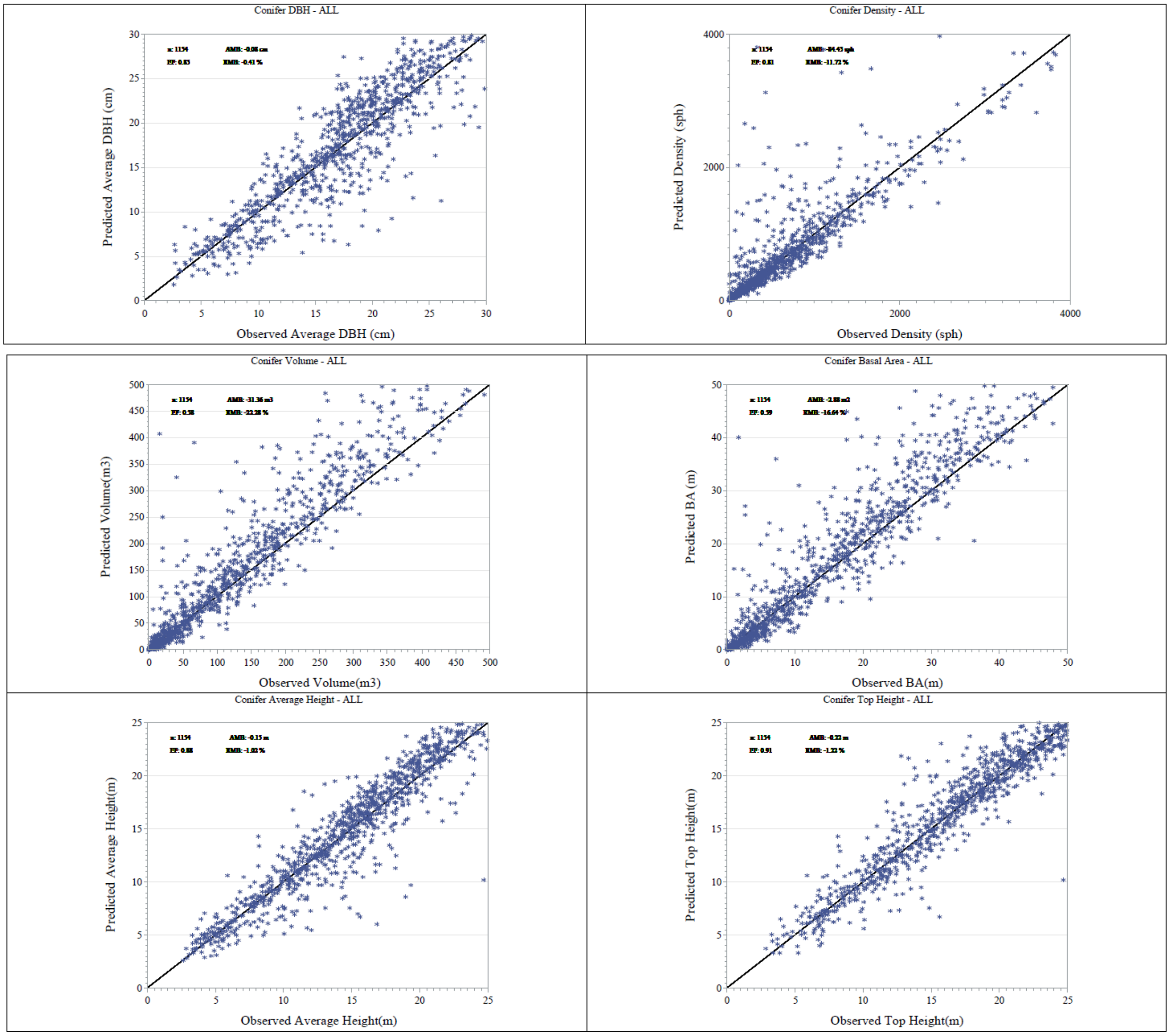

Figure 4.6 Scatter graphs showing values for MGM predictions for 6 variables plotted against observed values for the conifer component of the 1154 stands of the Alberta PSP dataset.

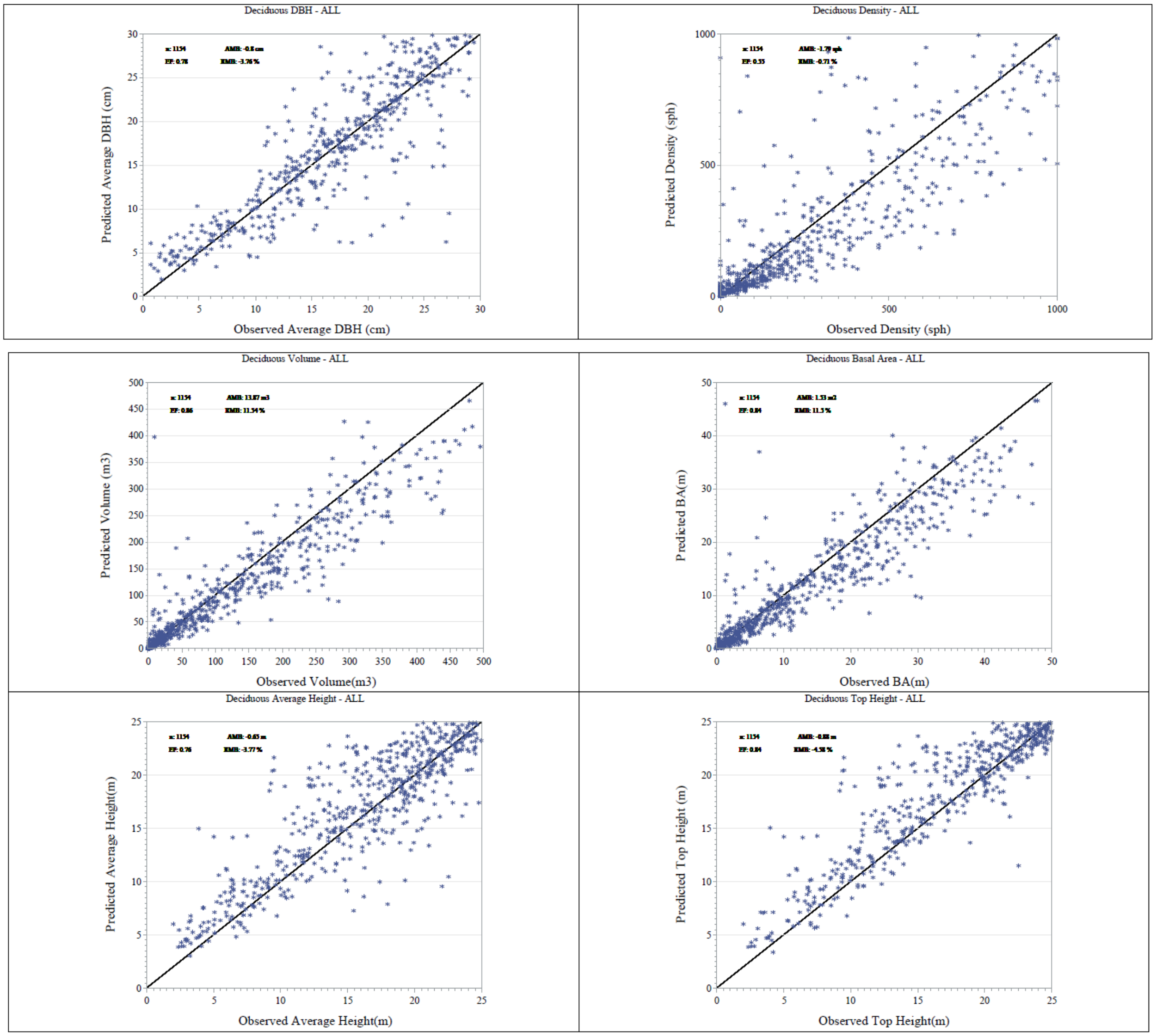

Figure 4.7 Scatter graphs showing values for MGM predictions for 6 variables plotted against observed values for the deciduous component of the 1154 stands of the Alberta PSP dataset.

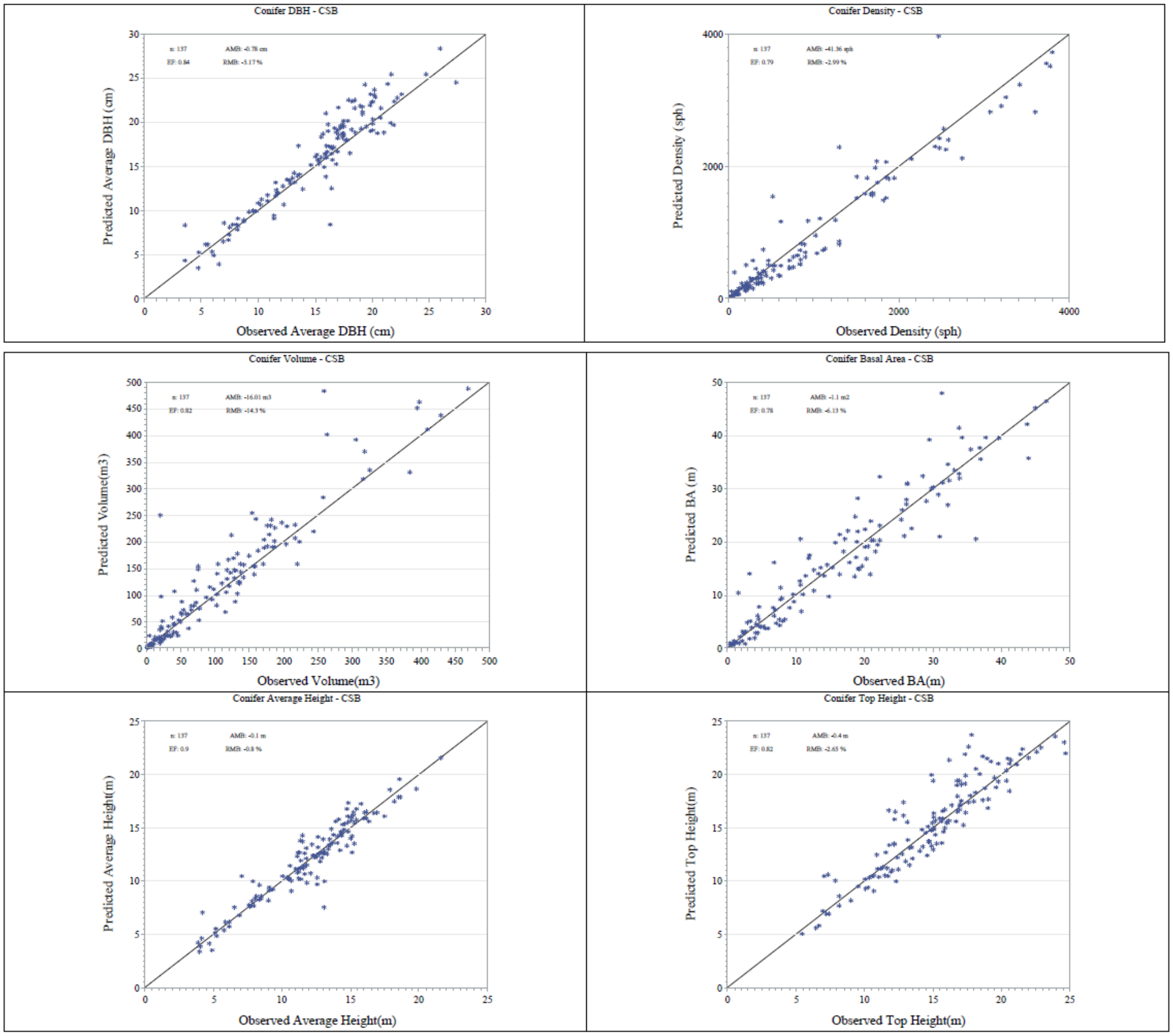

Figure 4.8 Scatter graphs showing values for MGM predictions for 6 variables plotted against observed values for the conifer component of the 139 simulated black spruce stands in the Alberta PSP dataset.

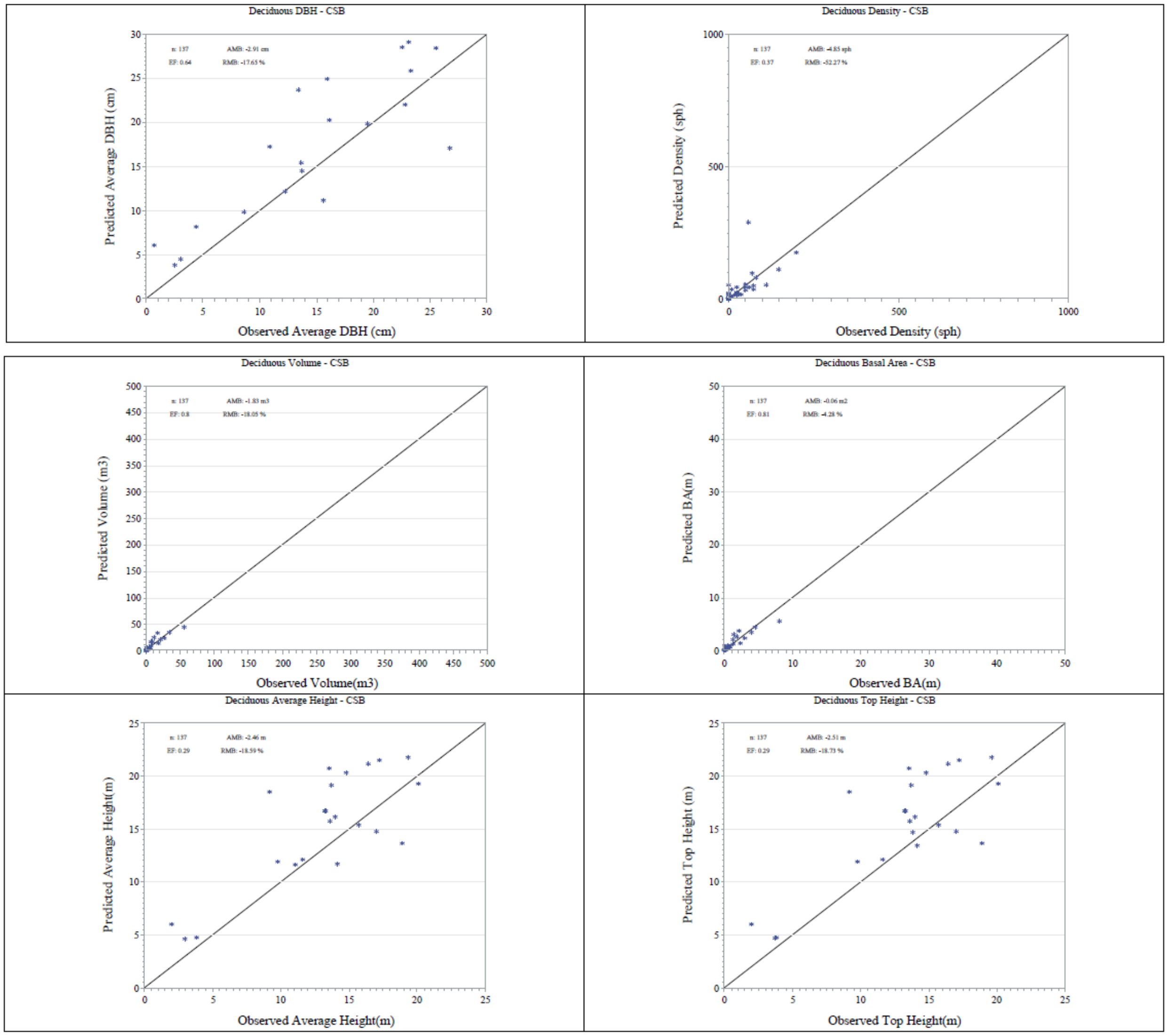

Figure 4.9 Scatter graphs showing values for MGM predictions for 6 variables plotted against observed values for the deciduous component of the 139 simulated black spruce stands in the Alberta PSP dataset.

4.3.2.2 Validation using Saskatchewan dataset

The validation dataset for Saskatchewan had 791 plots and the validation results are shown in Table 4.6 while the scatterplots are presented in Figure 4.10 and 4.11. For the conifer component, the RMB (%) values were less than 10% except for volume (-12.24%) and efficiency were all more than 0.65. The RMB(%) of the deciduous component were all less than 10% and the efficiency were all more than 0.80.

The validation dataset contained 125 plots from Saskatchewan that were considered pure black spruce, those containing more than 80% conifer basal area from the Saskatchewan dataset. The scatterplots of the observed and predicted values for all the analyzed variables can be found in Figure 4.12 and 4.13. An overview of the AMB (average model bias), RMB (relative model bias) and EF (efficiency) for the selected variables can be found in Table 4.7. When assessed graphically (Figure 4.12), conifer stand volume and basal area are largely unbiased with a slight over-prediction shown in the scattergraphs when compared to the 1:1 line. Conifer DBH is overestimated and conifer density is underestimated by 7.25 and 9.59%, respectively. Stand volume prediction showed a small RMB (-4.29%) and an efficiency of 0.85. Stand basal area had an RMB of -4.44% and an efficiency of 0.84. Average height has a very low RMB (0.5%) and a high efficiency (0.90). Top height has a RMB of 3.70% and an efficiency of 0.82. Average DBH has a low RMB (-7.25%) and moderate efficiency (0.50). For the minor deciduous component MGM is predicting deciduous volume in these stands well but is underestimating deciduous densities by about 25 stems/ha (Table 4.7 and Figure 4.13). The RMB for deciduous volume is very low (0.47%), while RMB for deciduous density is very high (42.90%) due to the small numbers of aspen in these stands. However, efficiencies for these variables are high (0.96 and 0.84, respectively). MGM is overestimating deciduous DBH, height and top height by 13.05%, 11.51%, and 9.77%, respectively, with moderate (0.39 - 0.53) efficiency.

Table 4.6 Means, ranges and standard deviation(SD) for observed and model fit statistics for selected conifer and deciduous variables based on simulations for 791 Saskatchewan PSP's plots using MGMvs 2017 A1 (Rev5712).

	Conifer							Deciduous						
	Observed				Statistics of Model Fit			Observed				Statistics of Model Fit		
Variable	**Mean**	**Min**	**Max**	**SD**	**AMB**	**RMB(%)**	**EF**	**Mean**	**Min**	**Max**	**SD**	**AMB**	**RMB(%)**	**EF**
Volume (m^3/ha)	186.83	0.94	532.88	98.30	-22.86	-12.24	0.66	99.51	0.28	443.82	93.31	3.83	3.85	0.85
BA (m^2/ha)	23.72	0.19	54.41	11.23	-2.18	-9.21	0.73	11.17	0.06	42.93	9.69	0.61	5.43	0.85
DBH (cm)	19.92	10.55	49.28	6.05	-0.02	-0.11	0.92	22.45	7.70	46.70	6.74	-0.51	-2.28	0.85
Height (m)	17.31	9.36	32.19	3.64	-0.46	-2.68	0.86	19.52	8.7	29.85	4.06	-0.38	-1.93	0.81
Density (sph)	867.36	0	4166.67	714.99	-14.26	-1.64	0.93	226.34	0	2262.5	318.82	18.15	8.02	0.87
Top Height (m)	20.89	9.73	36.14	4.57	-0.14	-0.67	0.88	20.55	8.7	31.85	4.33	-0.50	-2.42	0.82

Table 4.7 Means, ranges and standard deviation(SD) for observed and model fit statistics for selected conifer and deciduous variables based on simulations for 125 Saskatchewan PSP's dominated by black spruce using MGMvs 2017 A1 (Rev5712).

	Conifer							**Deciduous**						
	Observed				**Statistics of Model Fit**			**Observed**				**Statistics of Model Fit**		
Variable	**Mean**	**Min**	**Max**	**SD**	**AMB**	**RMB(%)**	**EF**	**Mean**	**Min**	**Max**	**SD**	**AMB**	**RMB(%)**	**EF**
Volume (m^3/ha)	184.45	18.23	421.17	90.34	-7.91	-4.29	0.85	19.16	0.35	123.33	23.93	0.09	0.47	0.96
BA (m^2/ha)	28.57	3.74	54.42	11.63	-1.27	-4.44	0.84	2.86	0.09	16.70	3.15	0.26	9.18	0.94
DBH (cm)	13.73	10.57	19.56	1.84	-1.00	-7.25	0.50	18.72	9.80	32.90	5.04	-2.44	***-13.05***	0.48
Height (m)	13.69	9.36	18.41	2.24	0.07	0.50	0.90	15.39	8.70	21.73	3.07	-1.77	***-11.51***	0.39
Density (sph)	1843	297	4167	791	176.75	9.59	0.85	57	0	717	105	24.56	***42.90***	0.84
Top Height (m)	17.39	10.71	26.62	3.33	0.64	3.70	0.82	15.77	8.70	21.98	3.30	-1.54	-9.77	0.53

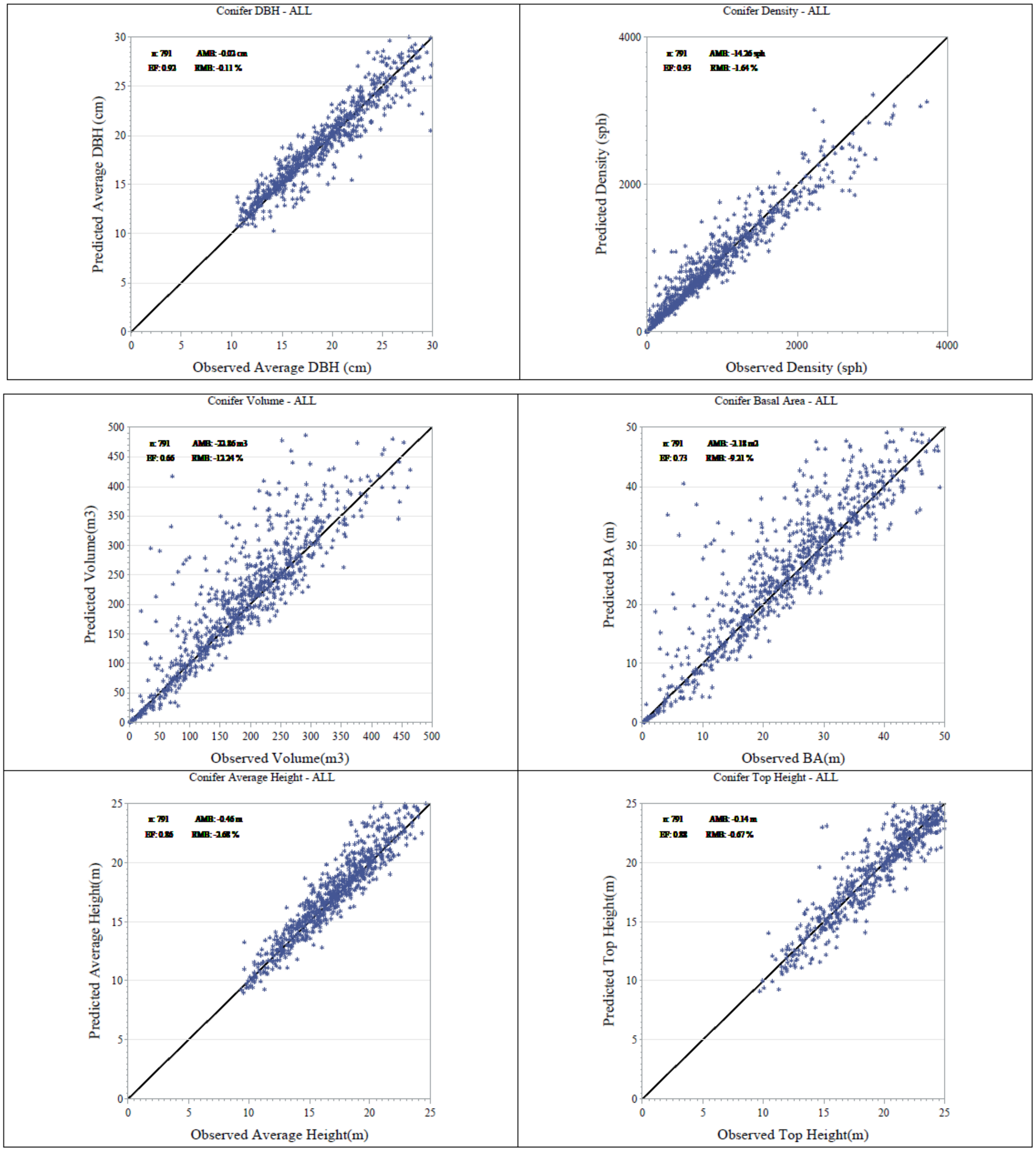

Figure 4.10 Scatter graphs showing values for MGM predictions for 6 variables plotted against observed values for the conifer component of the 791 stands of the Saskatchewan PSP dataset.

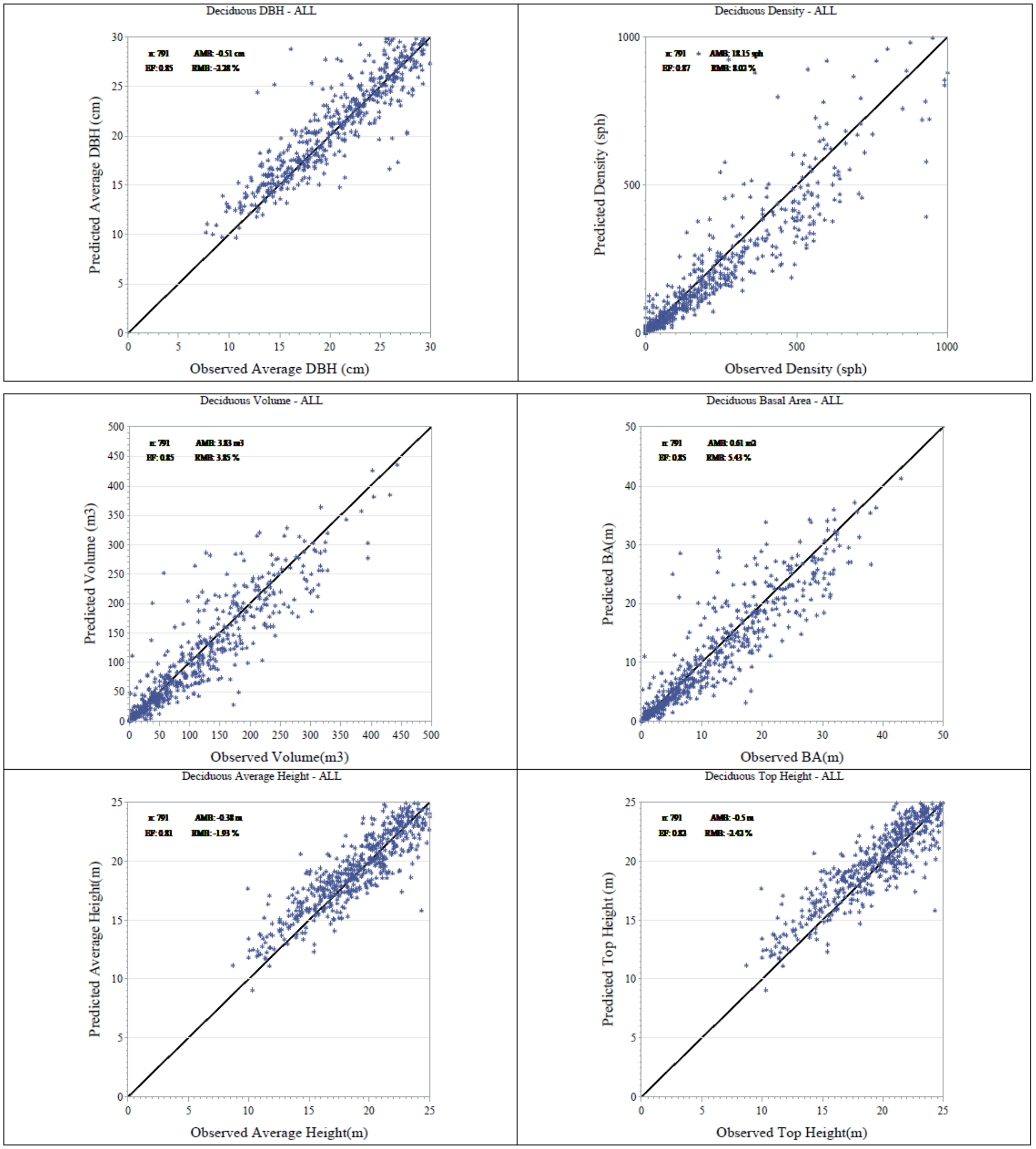

Figure 4.11 Scatter graphs showing values for MGM predictions for 6 variables plotted against observed values for the deciduous component of the 791 stands of the Saskatchewan PSP dataset.

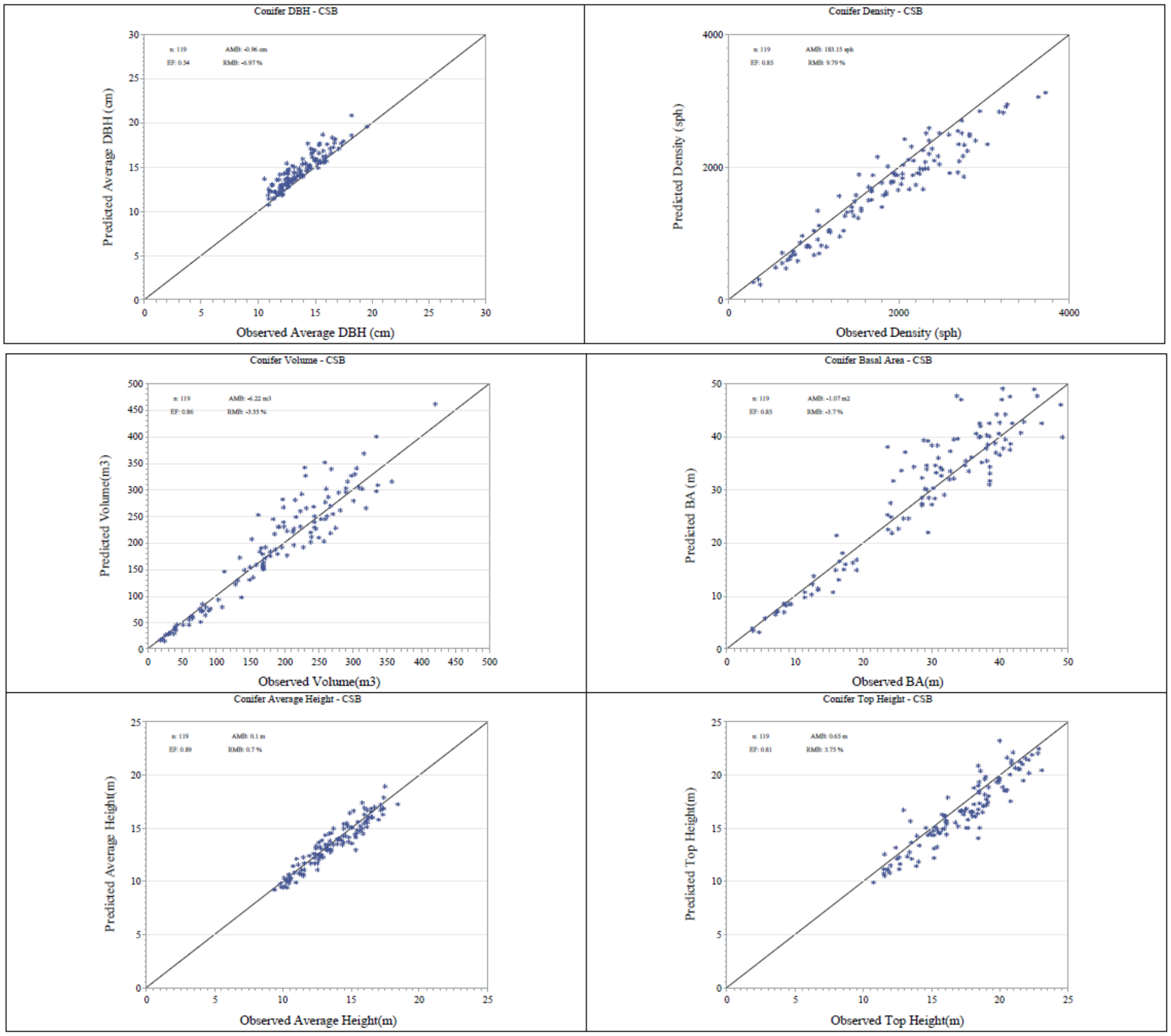

Figure 4.12. Scatter graphs showing values for MGM predictions for 6 variables plotted against observed values for the conifer component of the 125 simulated black spruce stands in the Saskatchewan PSP dataset.

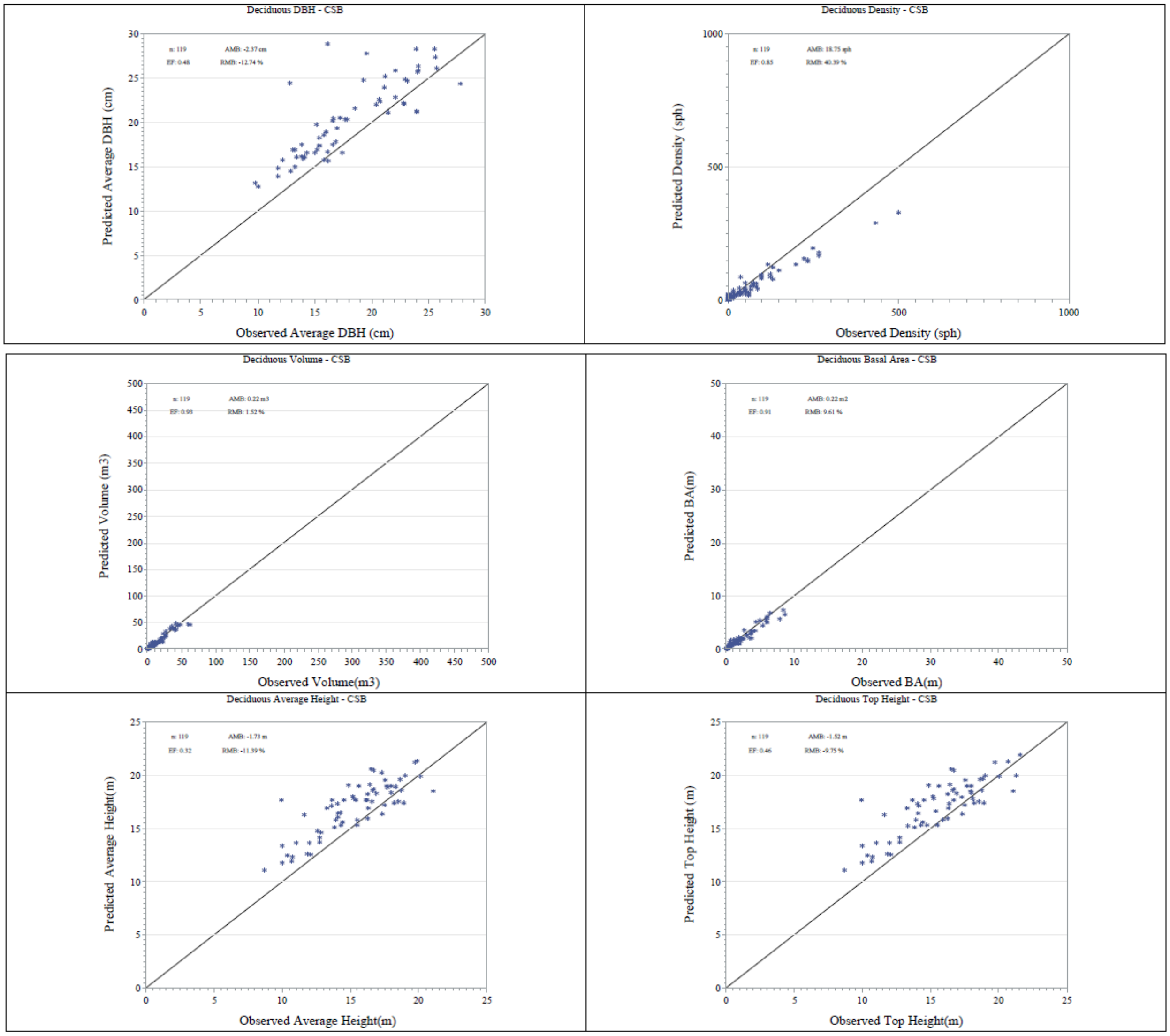

Figure 4.13. Scatter graphs showing values for MGM predictions for 6 variables plotted against observed values for the deciduous component of the 125 simulated black spruce stands in the Saskatchewan PSP dataset.

4.4 Discussion

4.4.1 Effect of splitting datasets for validation

Kozak and Kozak (2003) recommended that the full dataset should be used for model building and no data should be reserved for validation, however, splitting of dataset for validation is still a common practice. Issues related to reserving data for validation include: 1) whether validation data are really independent of the model fitting dataset; and, 2) what proportion of data should be reserved for validation. This study was designed to address the latter issue using black spruce data collected across provinces in western Canadian boreal forest and Alaska. The mean estimates of MAE and RMSE from 1000 bootstrap samples were consistent and sufficient for this study. A similar resampling method was used by McRoberts et al. (2011) where stability was observed in the standard error of the mean for 1000 bootstrap samples and not for 200 bootstrap samples which was originally recommended by Efron and Tibshirani (1994).

There was no difference in the performance of models developed with 90% and those developed with 50% (Table 4.3) as shown using paired t-test, KS and Wilcoxon (Huang et al. 2003). This might be a result of using the large dataset available for this study. This suggests that the 50% dataset was large enough to capture the trend in diameter growth in this area. In reality, there is a possibility of selecting a 50% dataset that might not represent the entire dataset but with appropriate randomization procedures the occurrence of such situations can be minimized.

Both validation metrics (MAE and RMSE) produced similar results for modelling and splitting datasets. The best model was the second model form (model 3 and 4) which was fitted with height increment. The difference in the performance of 90% and 50% datasets in model 3 was reduced in model 4 were MAT was included in the model. The effect of MAT in reducing the impact of reserving data was also similar for model form one and model form four. However, MAT increased the difference in the performance of the two datasets in model form 3. Generally, this result indicates that model form (performance of individual model) and variables included in model development are important factors that have greater effect on results than data splitting (Figure 4.4 and 4.5).

4.4.2 MGM Validation

The accuracy of individual models does not give enough information about its compatibility with other models (Huang et al. 2003). When models are incorporated into a growth and yield model like MGM, it is necessary to assess the accuracy of model. This gives the modeler an opportunity to assess the performance of the model as a system at an operational level.

Generally, the new version of MGM for black spruce performed well for all stand variables. When assessed graphically, conifer stand volume and basal area are largely unbiased with a slight over-prediction shown in the scattergraphs when compared to the 1:1 line. The deciduous stand volume and basal area showed a slight under-prediction. Efficiencies were generally high, which indicates that a large amount of variation in the variables is explained by the model. For plots dominated by black spruce, RMB's for the deciduous component were relatively higher than those for the conifer which is largely reflecting the small numbers of deciduous in these plots.

While RMB for conifer volume across the entire Alberta PGYI dataset is wide, this version of the model still has a narrower RMB than found with validation of the previous version of MGM for black spruce (Phil Comeau, Pers. Comm. February 1, 2018).

Assessments were done at the level of political jurisdiction (Alberta and Saskatchewan). For plots from Alberta (Table 4.4), the model had a relatively high bias for volume and basal area, with the maximum RMB being 22.28% for the conifer component. The efficiencies were also relatively high, with the exception of basal area and volume (conifer component) and density for the deciduous component. The relatively higher bias in conifer stand volume is mainly as a result of over prediction in some stands with low volume. This likely reflects either the lack of records of thinning activities in these stands, errors in the data, or the occurrence of undocumented stochastic events such as snow breakage, windthrow, or leader whipping. For the deciduous component there was under prediction in stand volume and basal area and over prediction in height and top height. This can happen due to the fact that the growth of the height is driven by site index in MGM, with a lack of reliable age data possibly inflating site index values.

For black spruce dominated stands in Alberta plots (Table 4.5), deciduous density has an RMB of ≈31%, but this is happening because the deciduous density is generally small and a small absolute bias translates into a large relative bias (sph (21.54) AMB(6.81) -> 31.57% RMB). There was small over prediction for other variables for the deciduous component which is due to low number of plots with deciduous.

For plots from Saskatchewan, the AMB and RMB are low for all the variables analyzed in the conifer component except volume (RMB 12.24%). However, in the deciduous components of plots dominated by black spruce, DBH, height and density were largely over predicted (Table 4.7). This is mainly due to the small number of plots with a deciduous component which is similar to results obtained in Alberta plots.

4.5 Conclusion

Black spruce is ecologically and economically important in the Canadian boreal forest and it is important to have reliable models to enhance forecast of pure and mixed black spruce stands across the landscape. Validation is a major part of model building and this study showed that models fitted with a smaller dataset (50%) after reserving dataset for validation have similar performance to model fitted with the large dataset (90%). Since the full dataset for this study is large, recommendation would be that a similar study should be done with a smaller dataset with application of more validation metrics. The validation of MGM for black spruce showed that recalibration with this large dataset resulted in an improved version of the MGM with better predictive ability. Validation was done on black spruce stands from the Alberta and Saskatchewan PSP dataset as well as for all stands included in the dataset. This updated version of MGM shows good performance in predicting stand volume, basal area, DBH, average height and top height for the conifer and deciduous component with minimal bias. Further refinements are needed to improve general performance of the model, including: development of species specific growth functions for balsam poplar, and development of growth functions for all species that include climate, and development of improved ingress functions.

Chapter 5: Conclusion and recommendations

Understanding how trees respond to natural disturbances such as mountain pine beetle (MPB), climate change and even competition helps us to create effective management strategies to ensure sustainable timber supply. Information from such tree growth responses provides the basis for developing reliable growth and yield models for making stand projections which would determine whether or not silvicultural interventions are required and what the stand volume will look like at a particular time in the future. This study covers a wide range of factors that affect growth and survival of black spruce especially under changing climatic conditions.

Chapter 2 of this thesis focused on improving our understanding of stand dynamics following MPB outbreak. Since regeneration of these stands would be a major concern (Mcintosh and Macdonald 2013; Campbell and Antos 2015) and timber supply is also greatly affected by MPB (Amoroso et al. 2013; Dhar et al. 2016b), this study provided valuable information about growth of advance regeneration of white spruce and black spruce in MPB affected stands as well as identifying important indicators of growth response. MPB outbreak increased diameter and height growth for both spruces and a delay in growth response was experienced by both spruces. It is assumed that this period is when the spruces develop new needles, adjust root:shoot ratios, and adjust to changes in the environment such as increase light, soil water, soil nutrient and space. In addition, this period also coincides with the changes of needle color and dropping of needle for the dead lodgepole pine tree approximately two to four years after MPB (Natural Resources Canada 2017). This process is gradual and differs from overstory harvesting which results in rapid changes in the environment of advance regeneration (Ruel et al. 2014). Black spruce had a longer diameter and height growth delay period (6 and 5 years respectively) after release than white spruce (4 and 4 years respectively).

Effective indicators of potential for release of advance regeneration are needed to inform management decisions in stands attacked by mountain pine beetle. In this study, I examined a number of indicators including tree sizes at the time of attack, pre-release growth rate, age and also stand factors like live tree basal area and spruce/fir basal area per hectare. Pre-release growth had a positive relationship with post-release growth. Post release growth rate was positively affected by tree size and negatively affected by age and spruce/fir basal area per hectare. Similar variables also affected pre-release growth rate except spruce/fir competition which only affected white spruce pre-release diameter growth rate. This result indicates that the low effect of spruce/fir competition before MPB attack might be as a result of the influence of the overstory lodgepole pine (combination of live and dead tree basal area). Growth ratio (ratio of postrelease to prelease growth) was also used to evaluate release response after MPB outbreak. As trees increases in release response to MPB (growth ratio), there was also an increase in post-release growth rate except for small trees with very high growth ratio (> 2.5 growth ratio for white spruce and ~1.8 for black spruce height growth ratio). Trees with high growth ratio are smaller trees (more suppressed trees) that show proportionally larger response to release than larger trees (Ruel et al. 2014). An important finding is that the level of suppression determines the amount of growth ratio response. Trees with smaller initial size are likely linked to more competition, therefore, they strongly respond because the change in light is more substantial than larger trees growing under less competition. Further studies should explore influences of tree crown size and leaf area and other indicators of suppression at the time of MPB outbreak.

Since only data from high mortality plots were analyzed, live tree densities were low and did not show any effect on growth responses and light due to the limited variation of live tree densities.

Ongoing monitoring of these trees is needed to evaluate long-term responses. Understory light was shown in this study to be associated with spruce/fir competition and spruce/fir competition measured within 5.64m radius was a better predictor of light than densities measured within 3.99m radius. Results also revealed that, while spruces have the potential to replace dead lodgepole pine trees, thinning and other treatments may be needed in areas with high spruce/fir competition.

I recommend continued monitoring and remeasurement of these PSPs to build on our present information. Further work will need to be carried out on wet sites as results indicate that one of the sites experienced some negative growth after release which might be due to an increase in soil water (wetting up) associated with MPB outbreak. When selecting MPB attacked stands for understory retention the quantity of advance regeneration should also be reasonable. I would recommend that further studies be undertaken to explore the effects of understory spruce stocking (ie. stand density) on growth and yield using model like MGM. Such information would be useful in guiding decisions such as whether clearcutting and reforesting may be better options than relying on growth of advance regeneration.

Chapter 3 addressed recalibration of the mixedwood growth model (MGM) and included development of diameter and height growth and mortality functions. Fitting of these models were necessary to improve predictions for black spruce in the western Canadian boreal forest. Important competition variables including deciduous, spruce/fir and pine were included and their influence on growth and mortality were examined. Since black spruce is a shade tolerant tree species, they can naturally grow as pure and mixed stands and it is important to capture their growth and mortality under these varying conditions in MGM (Bokalo et al. 2013) so that model performance can be satisfactory across these conditions. Deciduous competition was associated with increased growth while spruce/fir and pine competition decreased growth with spruce/fir having the strongest effect. On the other hand, effect of spruce/fir competition on mortality was the weakest while pine was the strongest. This likely results from overtopping pine and deciduous being taller than overtopping spruce/fir and consequently having more influence on light than spruce/fir competition.

Assessment of models is regarded as a continuous exercise (Shifley et al. 2017) and modellers should continuously strive to improve the quality of their model. Therefore, as a way of improving MGM especially on a large dataset that cut across western Canada, was to include important climate variables in the model (Manson et al. 2015). Several climate variables were tested. Temperature related variables (MAT, FFP) generally support growth (Gennaretti et al. 2014) while moisture related variables (MAP, CMI) reduced growth of trees. Black spruce often grows in wet sites where an increase in water could be detrimental to growth. For best diameter, height and mortality equations, MAT, CMI and MSP were the strongest predictors, respectively. The effect of climate variables was supported by other studies that used the same dataset across western Canada, e.g. Cortini et al.(2017) mortality equations include CMI and Comeau et al. (in preparation) max density functions include MAT and these climate variables were found to be very significant.

The use of height-diameter relationships (compatible growth model) to fit the diameter growth model in MGM was also examined, and the effect of competition and climate on this relationship. Compatibility is a method MGM uses to connect all models together to ensure consistency in prediction (MGM, Bokalo et al. 2013). There is ecological significance in considering compatibility, for instance the relationship between diameter growth and height growth is dependent on stand conditions (Nunifu 2009) and environmental factors and this determines the diameter and height of the tree. However, the argument that compatibility can also affect a model negatively by putting constraints on the model (Ochi and Cao 2003), was also supported in this study. Competition and climate influences on growth also affected the diameter-height and diameter-volume growth allocation. Spruce/fir competition more strongly affected diameter-height growth allocation than diameter-volume allocation. Increase in MAP increases growth allocation to diameter than height while increase in CMI increased growth allocation to diameter over volume.

One limiting factor encountered in this study was the absence of site index data for black spruce which could have been used to estimate potential growth of trees (Nunifu 2009) in place of potential maximum height (HImax). This is as a result of the difficulty associated with estimating site index of trees growing in the understory. Therefore, the use of other geocentric estimators (such as climate, soil drainage) or other approaches need development.

In chapter 4, the effect of reserving data for validation on model performance was explored. In this study the large black spruce dataset was used to compare the difference in model performance between 90% dataset and 45% dataset. The large dataset used in this study provided an opportunity to explore diameter growth of black spruce over a wide range of stand conditions including densities, climate, site condition and tree sizes. Results revealed that splitting data and reducing the size of the calibration dataset did not affect model performance, however, slight differences between the model performance between the resulting datasets were evident across model forms and depended on variables included in the model. I would recommend that further studies should be carried out using a volume model (since it captures diameter and height growth), smaller datasets, more model forms and with inclusion of climate. When validating a complex system of equations used in a model such as MGM, reserving data might not be necessary since the performance of the entire system is more important than performance of submodels (Huang et al. 2003). Validation in MGM is often done by using the entire dataset used for model building (Bokalo et al. 2013). All individual components (sub models) were incorporated into MGM and validation revealed that the new version of MGM is an improvement over the former. There was a slight over prediction in stand volume and basal area for the conifer components for both the Alberta and Saskatchewan datasets, however, these biases were small. This clearly shows that the new version of MGM can reliably simulate black spruce growth across a range of stand conditions in western Canada. Further work on MGM is needed to refine the model and reduce biases and might be best focused on improvements in site index estimation, refinement of growth functions for species other than black spruce, and inclusion of climate and site variables in growth and mortality functions.

Finally, this study contributes to knowledge by: (1) Identifying indicators of release for black and white spruce following MPB outbreak, which could be used by forest managers to improve management decisions regarding which trees or stand to be retained; (2) Developing quantitative equations for black spruce that enhance the predictive ability of MGM to make better stand growth and yield projections and improve silvicultural interventions across four western Canadian provinces and Alaska; (3) Improving the current understanding of growth allocation to diameter, height and volume under varying competition types and tree sizes; and, (4) Examining the effect of data reservation during model development on model performance.

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